

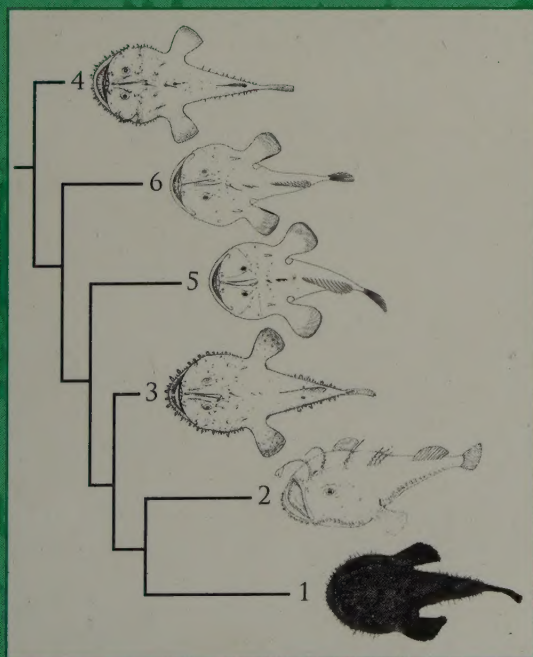
OXFORD BIOGEOGRAPHY SERIES Nº 12

CLADISTIC BIOGEOGRAPHY

SECOND EDITION

INTERPRETING PATTERNS
OF PLANT AND ANIMAL
DISTRIBUTIONS

CHRISTOPHER J. HUMPHRIES
AND LYNNE R. PARENTI



OXFORD BIOGEOGRAPHY SERIES

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Interpreting Patterns of Plant
and Animal Distributions

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Preface

It was well understood by biologists in the eighteenth century that different plants and animals had particular distribution patterns over the surface of the earth. Since that time, literally thousands of biogeographical explanations have been published to account for the patterns but with varying success as to what those patterns mean. Perhaps most important, so forcefully pointed out by the botanist and biogeographer Leon Croizat, was that many of the clear-cut distribution patterns showed congruence when viewed on a broad, often global, scale. These 'generalized tracks' of distribution are so consistent in disjunct, trans-oceanic terrestrial taxa, such as flowering plants, mammals, and freshwater fish, that they imply historical connections between the biotas.

Analysis of biotic components to infer hierarchical classifications of areas using cladistic techniques is the method identified in this book as cladistic biogeography. This method is used to assess the significance of distributional congruence in relation to palaeogeography and geology, particularly in the southern hemisphere, including around the Pacific basin. General patterns of area relationship inform our understanding of the phylogenetic and distributional history of all life on earth, freshwater and marine, terrestrial and oceanic, fossil and Recent. A search for general patterns, of both plants and animals, remains our common goal.

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C. J. H.
L. R. P.

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The cover illustration shows six northern species of the marine teleost fish genus *Lophius*. From top to bottom these are *L. vaillanti*, *L. gastrophysus*, *L. americanus*, *L. budegassa*, *L. piscatorius*, and *L. litulon*. Illustrations are reproduced with permission from the following sources:

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Introduction

Biogeography means many things to many people depending on their outlook and purposes of enquiry. As data accumulated over the last two centuries it became clear that organisms exhibit particular distribution patterns over the surface of the earth. Given that picture, biogeographers ask the question 'What lives where and why?' The answers given invoke either ecological or historical explanations, or both.

Ecologists consider distribution patterns as communities at various levels of organization: species live in habitats belonging to ecosystems within biomes. For ecologists, biogeography seems to be subsidiary to ecology. Indeed, as Ball (1976) points out, some ecologists, such as MacArthur and Wilson (1967), do not see any distinction between the two subjects. Or, the distinction between historical biogeography and ecological biogeography has been considered one only of scale (e.g. Brown and Gibson 1983; Hengeveld 1990; Brooks and McLennan 1991). We think no one would disagree that many similarities of climate, topography, and physiognomy exist between, for example, the rainforests of South America and south-east Asia, but, when examined closely, the organisms living in each rainforest are generally quite different; similar species in similar ecological niches belong to phylogenetically disparate taxa that have unique phylogenetic and distributional histories and, therefore, demand different explanations. Some ecologists go so far as to say that the historical component is ecological (e.g. Flenley 1979; Stott 1981). This is because when examining dynamics of community structure—dispersion, on a local scale in a short time frame—changes in light, temperature, and humidity produce profound differences in relative frequencies of occurrence of species. Ecological biogeography neglects phylogenetic, major disjunct, and long-term temporal components which together comprise the elements of historical biogeography. Historical biogeographers focus on older events—the development of global biotas—in an effort to study the history of the earth rather than relatively more recent events such as, for example, short-term species interactions.

Data for historical biogeography come from comparative biologists and systematists who include distributional information in their monographs and revisions. A major synthesis is found in the work of Croizat, especially

in *Space, Time, Form: The Biological Synthesis* (1964)—a book of some 800 pages regarded by the author as a mere summary of his views. Croizat was a biologist who considered geological events and the ‘form-making’ of species parts of one historical process. Despite Corner’s (1959) perceptive observation that Croizat’s work is critical reading for anyone interested in the idea that the world and its biota evolved together, only during the last 25 years has greater notice been taken of his work. The interest has come at the same time as the gradual acceptance of plate tectonics and mobilist concepts of earth history, together with widening interest in the use of cladistics for phylogeny reconstruction—a method outlined formally by Hennig (1950, 1965, 1966) and developed by others (see particularly Nelson 1969, 1974). Expositions of the combination of the ideas of Croizat and Hennig can be found in Croizat *et al.* (1974), Ball (1976), Rosen (1976, 1978, 1979), Nelson (1974, 1978), and Nelson and Platnick (1981). Croizat (1982) emphasized strongly, however, that he never endorsed Hennig’s work on either cladistics or biogeography. Neither did he endorse the integration of cladistics with panbiogeography. As such, the cladistic concept of historical biogeography is separate from that of contemporary panbiogeographers such as Craw (1982), Heads (1985), Grehan (1991), and Craw *et al.* (1999) who follow Croizat’s method.

As Nelson (1978) and Nelson and Platnick (1980) point out, biogeography ‘is a peculiar discipline because most of its practitioners are not biogeographers but systematists specializing on some group of organisms’. In much the same way as systematists describe taxa and study their interrelationships on the basis of character distributions to discover what groups exist and what their origins might be, one could say that historical biogeographers study the distribution of taxa in different areas of the world to see how the areas are related, what regions or larger groups of areas exist, and what their origins might be (Platnick and Nelson 1978).

Concepts of regions or realms, of their relationship to each other, and of general patterns have changed during the history of biogeography. Ball (1976) and Patterson (1981a) recognize three phases of development in systematics (which Ball terms the descriptive phase, the narrative phase, and the analytical phase), all of which have influenced historical biogeography. An analogy may be drawn between the history of taxonomic methods and biogeographic methods. Descriptive, or alpha taxonomy, is the data-gathering enterprise of systematics which seeks to distinguish and describe taxa. Narrative taxonomy, by contrast, attempts to explain the evolutionary relationships of different organisms by using what may be called evolutionary systematic or omnispective methods for assessing groups by weighted similarities. Narrative taxonomy is still common to many undergraduate textbooks in which evolutionary relationships are presented as stories rather than as scientific hypotheses. Analytical

taxonomy here refers explicitly to cladistic methods as originated by Hennig (1950, 1965, 1966) and developed somewhat independently by Wagner (1961, 1980), Camin and Sokal (1965), Kluge and Farris (1969), and Farris (1970). Modern textbooks on cladistics include that of Eldredge and Cracraft (1980), but more important for biogeography, Nelson and Platnick (1981), Wiley (1981), Brooks and McLennan (1991), Wiley *et al.* (1991), Forey *et al.* (1992), and Kitching *et al.* (1998).

Historical biogeography has been associated mostly with the narrative and analytical phases of taxonomy, and can similarly be divided into narrative biogeography and analytical biogeography. Narrative biogeography is the practice of using historical (geological or climatic) events and various *ad hoc* assumptions, such as that all taxa have a 'centre of origin' and dispersed to other areas, as a basis for explaining distribution patterns. Analytical biogeography, by contrast, refers to the comparison of the pattern of relationship of different groups of organisms occupying similar areas to find biogeographic patterns.

Many names have been applied to analytical historical biogeography which emphasize explicitly the phylogenies of plants and animals; these include vicariance biogeography, cladistic biogeography, phylogenetic biogeography, historical biogeography, or, simply, biogeography. We have chosen 'cladistic biogeography' as the title of the method of analytical historical biogeography we endorse. It combines cladistics with historical biogeography, and has as its basic premise the search for patterns of relationships among areas of endemism.

Development of theory and methodology of biogeography has received attention from an increasing number of biologists and geologists during the past three decades. Our aim is to present a comprehensive review of the theory and method of cladistic biogeography, summarizing the historical changes leading to its formulation and presenting practical examples for systematists who may wish to undertake their own biogeographic studies. We have seen a renewed interest in biogeography during the past decade which, in large part, prompted the writing of this second edition of *Cladistic Biogeography*. Numerous biological journals have published special issues on biogeography, notably *New Zealand Journal of Zoology* (1989, 16 (4): panbiogeography), *Systematic Zoology* (1988, published 1989, 37 (3 and 4): vicariance biogeography), and *Australian Systematic Botany* (1991, 4 (1): austral biogeography; see Ladiges *et al.* 1991). The *Journal of Biogeography* has expanded its format, includes guest editorials that have proven to be a lively forum for debate, and developed sister publications such as *Biodiversity Letters* and *Global Ecology and Biogeography Letters*. Edited volumes have reviewed methodological developments (e.g., Hovenkamp 1987; Myers and Giller 1988) or biogeography of particular realms or taxa (Pierrot-Bults *et al.* 1986: pelagic seas; Liebherr 1988:

Caribbean insects; Woods 1989: the West Indies; Bănărescu 1990, 1992, 1995: freshwater animals; Goldblatt 1993: Africa and South America; Wagner and Funk 1995: Hawaiian islands). Principles of biogeography have a permanent place in conservation biology (Eldredge 1992; Forey *et al.* 1994). Explicit criteria for choosing areas to be conserved that incorporate biogeographic patterns have been proposed by Vane-Wright *et al.* (1991), Nixon and Wheeler (1992), and Stiassny and DePinna (1994).

The relationship between biogeography and geology (e.g. Sims *et al.* 1983, Leviton and Aldrich 1986; Briggs 1987a) or the fossil record (e.g. Smith 1994) has been the focus of regular review. Explicit plate tectonic interpretations of earth history have dramatically brought to attention the extreme geologic complexity of certain regions, such as the Indo-Australian archipelago (Daly *et al.* 1991), thus reinforcing the significant role of cladistic biogeography in inferring area relationships. The restricted ranges of both Recent (Hendrickson 1986) and fossil (Jablonski *et al.* 1985) taxa have been critical in identifying the boundaries of accreted terranes of western North America.

In Chapter 1, we concentrate on areas and distribution, the concept of regions and their relationship to each other, in a brief historical résumé. We outline main steps in the refinement of method in Chapter 2. In Chapter 3, we apply some of these methods to real taxa, in particular those of the marine realm to emphasize our view that cladistic biogeography need not be limited to terrestrial or freshwater groups. Finally, in Chapter 4, we examine one of the intellectual challenges of biogeography—a rational explanation for the history of the Pacific basin biota.

We prefer to call this book a monograph rather than a textbook. We have discussed and debated our ideas with colleagues who, in this case, are mostly practising biogeographers. We are, however, presenting our own interpretation of a field that has grown with the input from many of these colleagues, whose work we cite herein. Cladistic biogeography remains a changing field; we wrote the two editions of this book so that discussion, debate, and practice of biogeography may extend to a wider audience, to all systematic biologists.

1

Historical biogeography

1.1 INTRODUCTION

Our aim in this chapter is to review briefly the history of biogeography from Linnaeus to Croizat. The following three chapters detail subsequent critical developments in cladistic biogeography. The geographic distribution of living things has intrigued biological theorists, especially systematists, since the fifteenth and sixteenth century voyages of exploration brought to light exotic plants and animals. As the acquisition of specimens and the classifications based upon them improved, especially in the nineteenth century, botanists and zoologists tried to understand the burgeoning wealth of distributional evidence. As it became clearer that all organisms had particular distributions, enquiring minds tried to establish the historical causes of such patterns. Explanations of biogeographic patterns have varied by application of many and varied methods of analysis for different samples of taxa. Even for well-delimited areas, alternative approaches resulted in wildly different explanations. More recently, there has been a shift from attempting primarily to identify the processes that may account for present-day distributions to first identifying patterns. During the nineteenth century it became apparent that biogeographic explanations were tied to particular philosophical biases and couched in evolutionary, geological, or ecological views. Explanations of origin of taxa and evolutionary changes through time led to various notions; that all organisms originated from a particular place on earth, or that shifting continents account for large-scale patterns. Platnick and Nelson (1978 p. 8) succinctly argued that the fundamental issue facing biogeographers:

is not 'Is this pattern the result of vicariance or dispersal?' but 'Does this pattern correspond to a general pattern of area interconnections (and thus reflect the history of those areas) or not?' What is needed is a method of analysis that will allow us to determine whether two given distribution patterns correspond to each other or not, so that we can test the general hypothesis that the pattern of relationships of areas indicated by one group is a general one. After a hypothesized general pattern is corroborated, we may be able to ascribe it to a vicariance or dispersal by independent evidence of earth history.

Cladistic biogeography is a method of historical biogeography that fulfils many of the requirements of Platnick and Nelson's assertions. Cladistic biogeography combines Hennig's (1950, 1966) notion of relationship with distribution patterns to ask the question 'Are areas of endemism inter-related among themselves in a way analogous to the interrelationships of the species of a certain group of organisms?' In other words, of three different areas definable by the distributions of endemic taxa occurring in those areas, are two of them more closely related to each other than either is to the third? Such a question is part of a historical tradition of empirical enquiry which started in the work of Humboldt and Candolle, and was greatly developed by Croizat. It is part of a tradition that emphasized explanation of existing patterns in a general framework that accounts for all observations. It is an alternative to narrative dispersal biogeography which has its roots in the works of Linnaeus, Darwin, Wallace, and Simpson, which proffered interpretations of the underlying processes to account for the present-day patterns. Here, we attempt to describe the differences between the two approaches.

1.2 DISTRIBUTION PATTERNS

Every taxon, regardless of rank, has a particular distribution on the earth. Taxa vary in extent and degrees of continuity of geographical range, patterns of occurrence, and ecological requirements (see Gaston 1994). For example, consider the natural distribution of the dandelion, *Taraxacum magellanicum*, in the southern hemisphere. The map (Fig. 1.1) shows a fragmented distribution separated by oceans and the black areas represent the boundary limits of the species. The second map (Fig. 1.2) shows the sub-cosmopolitan distribution of the waterweed hornwort, *Ceratophyllum demersum*, occurring on all major continents. Exact localities are indicated only for a few areas, that is, northern Canada, Caribbean, and western Pacific; the range is shown by the black areas. There are conspicuous gaps on the map from which one can only conclude that waterweed hornwort is an aquatic species absent from dry areas and vast areas in Africa, South America and New Zealand that belong to Gondwanaland. The third example is the distribution of the North American–South American species *Osmorhiza chilensis* of the carrot family (Umbelliferae) (Figs 1.3 and 1.4). The map (Fig. 1.3) is generalized, showing the limits of distribution in western North America and South America and scattered localities across temperate North America.

Of course, all three species survive and reproduce in accordance with their own ecological requirements and life-history parameters. One does not find, nor expect to find, a freshwater angiosperm living with the Arctic terrestrial dandelion, and neither co-occurs with the umbellifer, *Osmorhiza*.



Fig. 1.1 Distribution of *Taraxacum magellanicum* (Asteraceae) (after Croizat 1952, Fig. 9).

Each of these three species occupies a precise area. Examination of each individual pattern would determine the environmental parameters that bound the distributions, but tell us little as to why there are massive disjunctions or what particular historical events could account for the present-day distributions.

Our observations need not be limited to one particular taxonomic rank. Disjunctions are true also for groups of species, genera and families. Consider the generalized distribution of *Acaena* (Rosaceae), a large genus of some 100 species of mostly herbs living in south temperate areas, Antarctica, the Andes, Hawaii, and California (Fig. 1.5). Many species have similar, but not necessarily completely overlapping, continental disjunctions as does *Taraxacum magellanicum*. We may ask

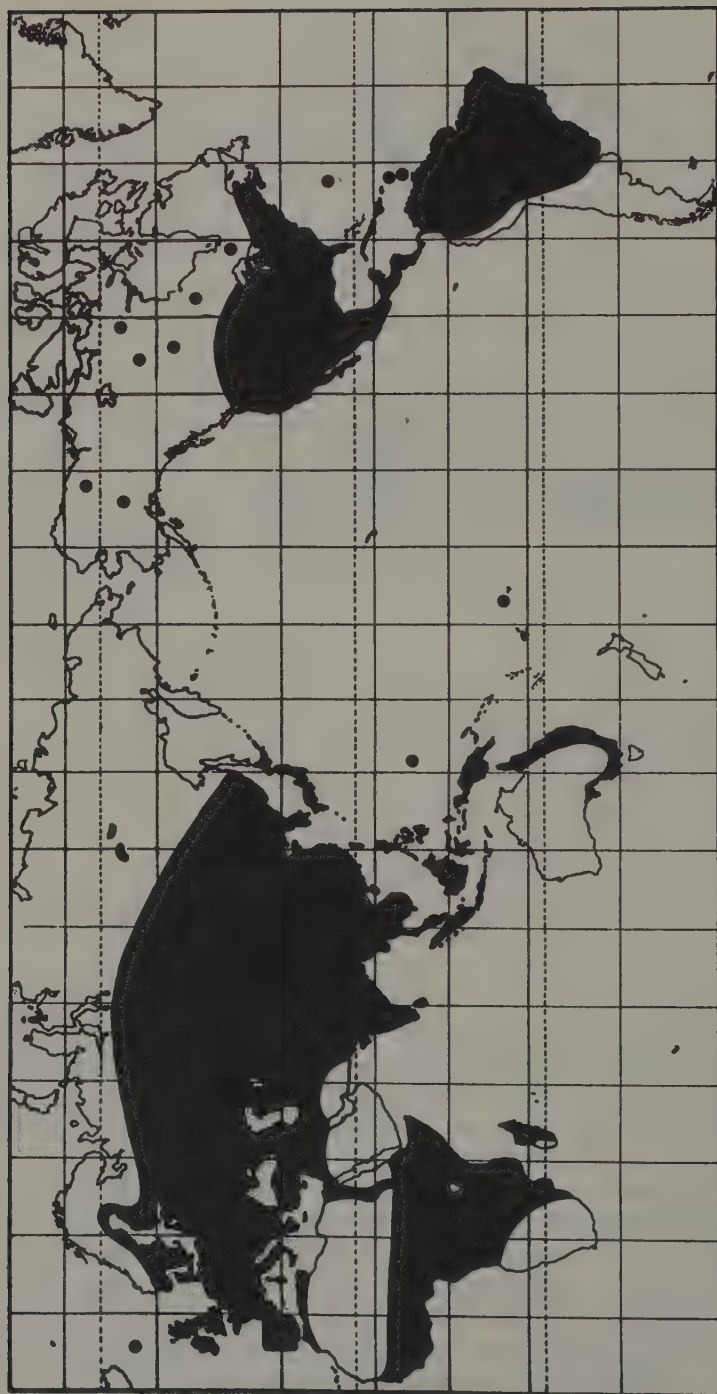


Fig. 1.2 Distribution of *Ceratophyllum demersum* (Ceratophyllaceae) (after Thorne 1972, Fig. 43, p. 397).

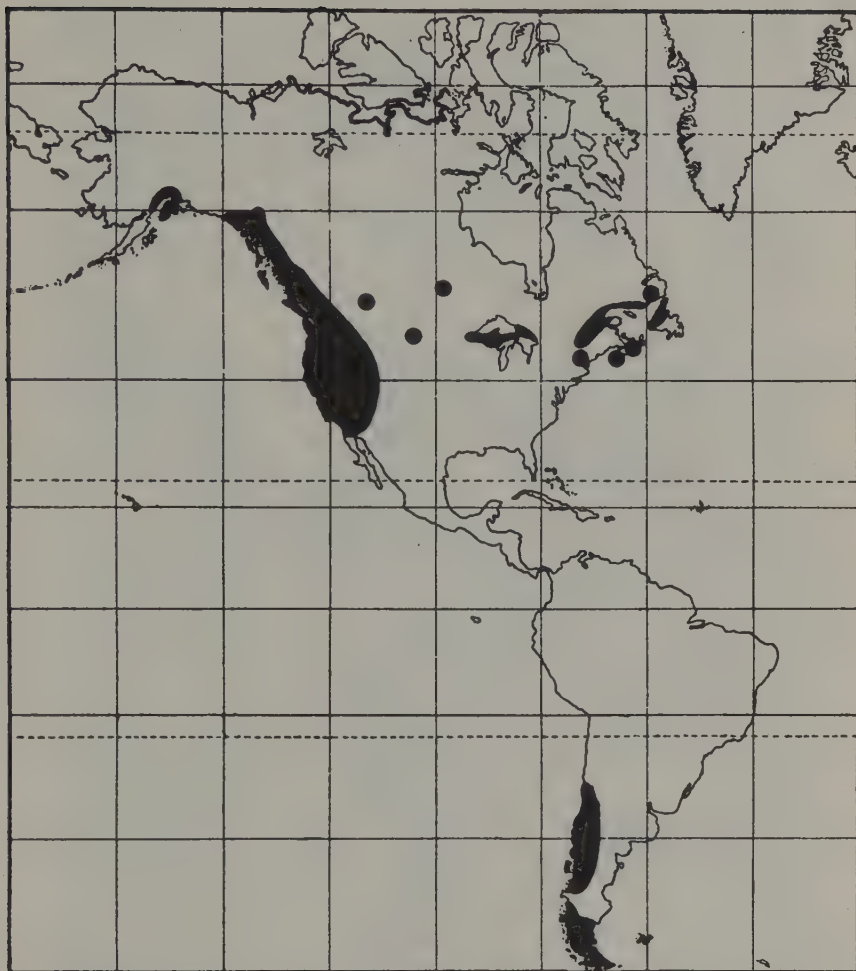


Fig. 1.3 Bipolar distribution of *Osmorhiza chilensis* (Hook and Arn), a member of the carrot family, Umbelliferae (after Thorne 1972, Fig. 35, p. 393; see Fig. 1.4).

whether *Taraxacum magellanicum* and *Acaena* had a similar biogeographic history to now show a similar continental distribution pattern, even though the areas each occupies at a finer scale hardly overlap at all. Harold and Mooi (1994) indicate that geographical congruence is recognized at different scales. We could consider the scale of relationships of South America, Africa, and New Zealand; *Taraxacum magellanicum* and *Acaena* show geographical congruence, but we can say little as to whether



Fig. 1.4 *Osmorhiza chilensis* (Hook and Arn). A member of the carrot family (Umbelliferae) with a bipolar distribution in North and South America (see Fig. 1.3; de Wildeman 1905, Plate iv).

this is meaningful at a finer taxonomic, hence distributional, scale, such as for example, distribution of species along mountain ranges within South America.

As a second example, the map in Fig. 1.6 shows the generalized distribution of the freshwater and coastal portion of the widespread marine and freshwater fish family Gobiidae. This group occurs in much the same parts

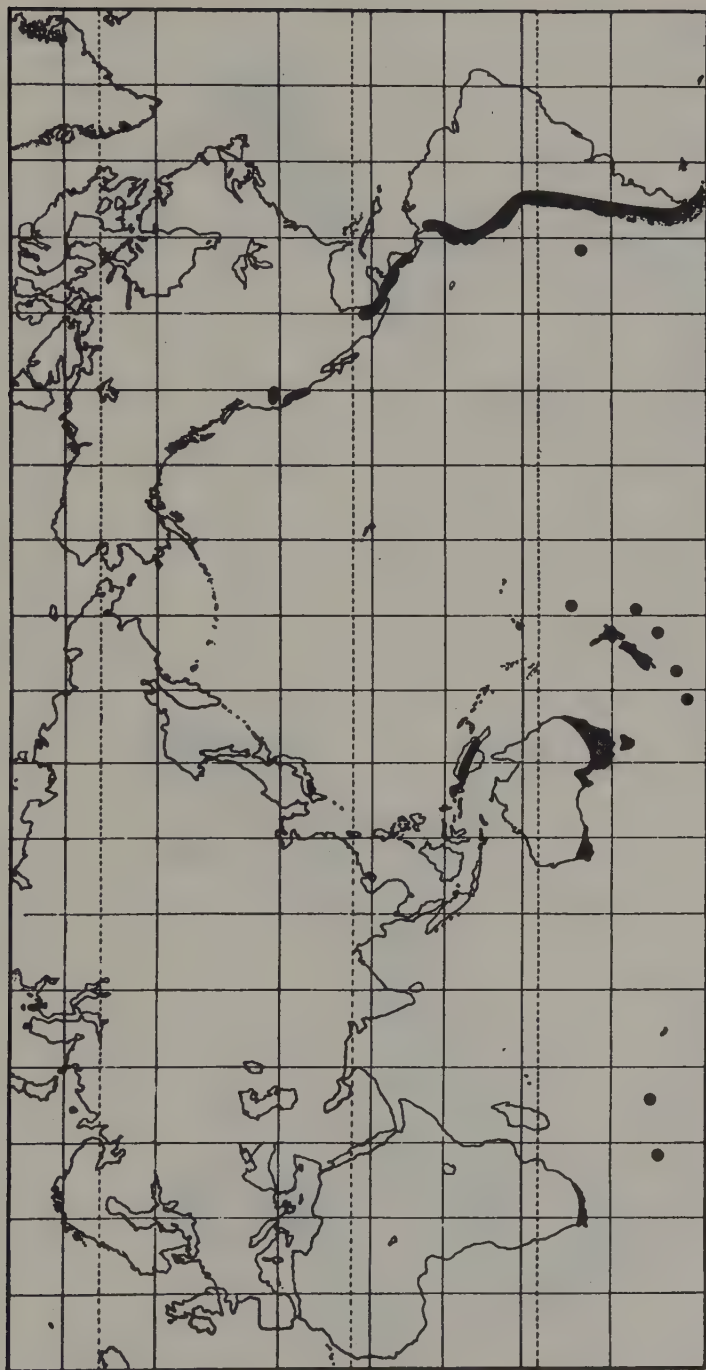


Fig. 1.5 Distribution of the genus *Acaena* (Rosaceae) (after Thorne 1972, Fig. 41, p. 396).

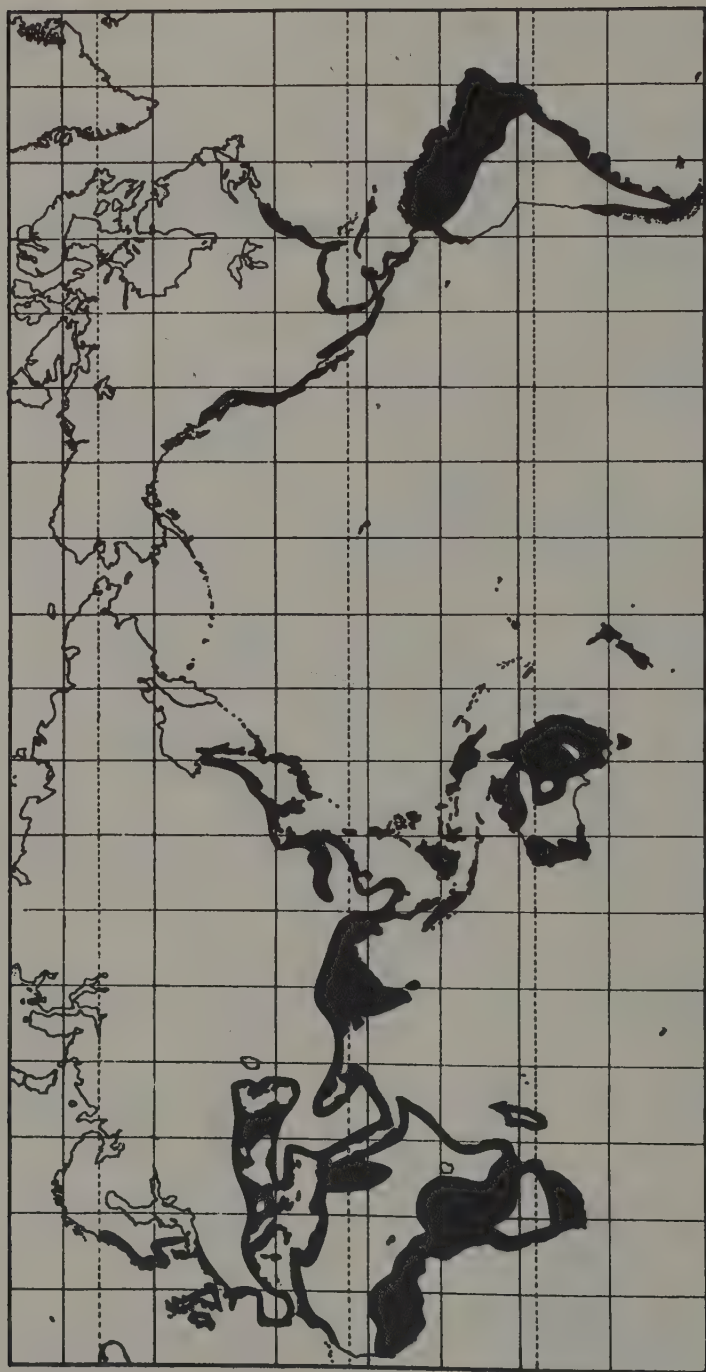


Fig. 1.6 Distribution of the freshwater and coastal marine fishes of the family Gobiidae (after Berra 1981).

of the tropics and warm temperate areas as does *Ceratophyllum*, but their distributions differ in northern and southern cool temperate areas. Finally, consider the distribution of the crowberry genus *Empetrum* (Fig. 1.7), with just two species occurring in a disjunct bipolar distribution. The range of the southern crowberry, *E. rubrum*, corresponds almost exactly to the southern populations of *Osmorhiza chilensis* (Fig. 1.3). The northern crowberry, *E. nigrum*, has a range that partially overlaps that of *Osmorhiza* but is more widespread throughout North America, Eurasia, and even the Arctic. In both examples, there is a fair degree of geographical congruence at the broad continental scale but little can be said about the relationships of those areas in the absence of more precise phylogenetic and distributional data.

Although the individual distributions of each taxon have been mapped and each has unique ecologies, some other kind of information is required to account for the sympatric occurrence of the highly divergent taxa. For any taxon we acquire details of distribution patterns slowly. We often have only the vaguest impressions of distribution patterns, and maps are compiled from different collections of historical evidence. Despite the vagaries of distribution map compilation, however, for any one taxon we have sufficient evidence to show that many patterns are repeated by distantly related taxa. For example, the temperate southern hemisphere regions of South Africa, southern South America, Australia, Tasmania, and New Zealand, together with the islands of subtropical New Caledonia and tropical New Guinea, show many strikingly similar allopatric disjunctions in related taxa. Distantly related taxa in any one region are sympatric (see Table 1.1). To us, the interesting aspect of individual distributions is that they are almost always part of a more general distribution pattern.

General distribution patterns are recognized at particular scales. For example, the disjunct patterns of the southern hemisphere (e.g. between Australia, Chile, and New Zealand) are most easily seen between species within a genus, or subspecies within a species. Redundancy in the patterns is more easily perceived between different genera within a family or families within orders, and so on. Thus, trans-Antarctic sympatric patterns between the major southern hemisphere continents are at the family level or above. The southern beech genus *Nothofagus* (Nothofagaceae) is broadly sympatric with the Winteraceae family, a distantly related group of angiosperms, and more remotely sympatric with several different groups of chironomid midges (see Table 1.1).

Disjunct vicarious distributions occurring repeatedly in different groups for the same areas are not confined to the southern hemisphere, but can be found all over the globe (Table 1.2). Classifications of intercontinental disjunctions for plants are found in Croizat (1952), Good (1964, 1974) and Thorne (1972). Individual distributions, although sometimes widespread,

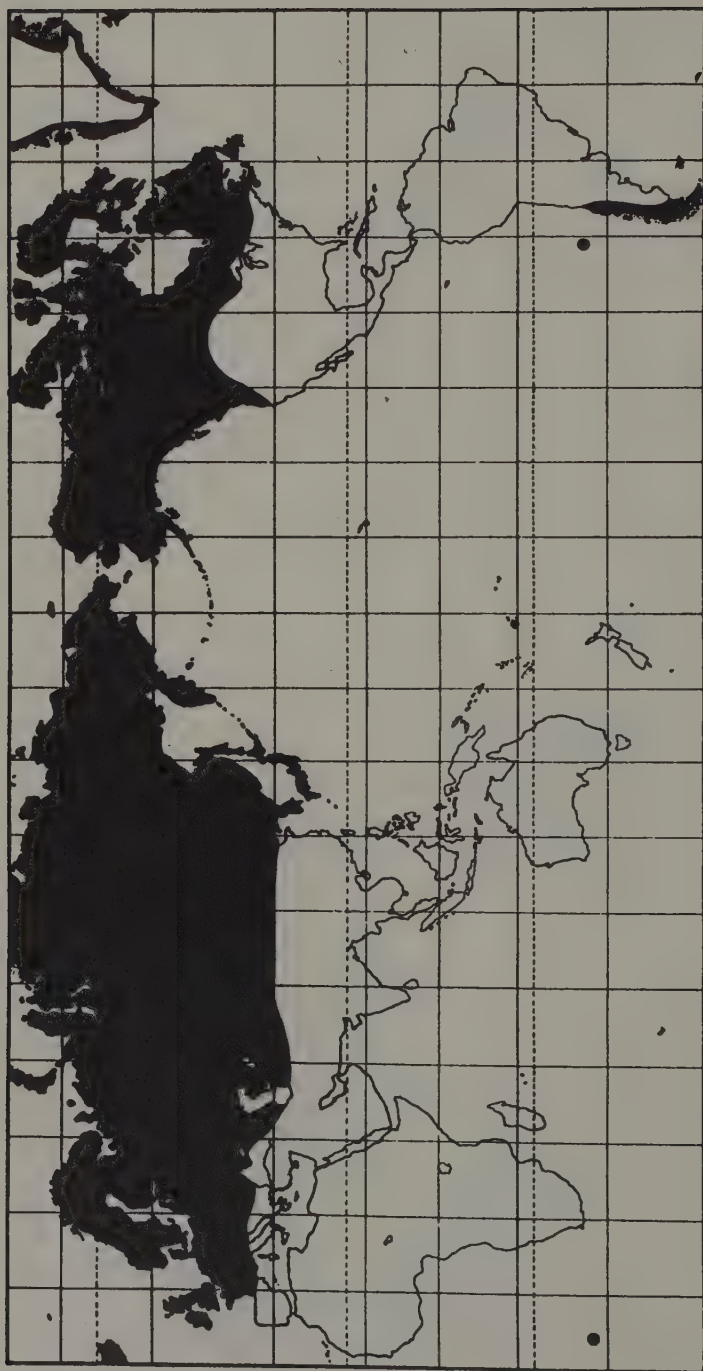


Fig. 1.7 Distribution of the genus *Empetrum* (Empetraceae) (after Thorne 1972, Fig. 36, p. 393).

Table 1.1 Distribution of endemic taxa in South America (SA), Africa (Af), Madagascar (M), Tasmania (Tas), Australia (Aus), New Zealand (NZ), New Guinea (NG) and New Caledonia (NC)

Family/genus	Areas								
	Af	M	SA	Aus	Tas	NZ	NG	NC	Others
Chironomid midges	+	+	+	+					1, 2
Winteraceae		+	+	+	+		+	+	3, 5
<i>Coriaria</i>			+			+	+	+	1, 2, 3, 4
Proteaceae (<i>Gevuina</i> , <i>Lomatia</i> , <i>Oreocallis</i> and <i>Orites</i> combined)				+	+		+		
<i>Acaena</i>	+		+	+	+	+	+	+	3
Osteoglossine fishes			+	+			+		
Ratite birds			+	+			+		2
Stylidiaceae			+	+	+	+			
<i>Nicotiana</i>			+	+				+	1
Hylid frogs and <i>Chaleosyrphus</i> (Syrphid flies)				+				+	1, 2
Marsupials (recent)			+	+			+		1
<i>Nothofagus</i>			+	+	+	+	+	+	

Other areas: 1, North America; 2, Europe; 3, Central America; 4, China/Japan; 5, Malaysia.

usually have more narrow ranges when viewed on a map of the world. Many taxa fall into a pattern of areas of endemism, especially apparent when a group of species is confined to one portion of a continent, an oceanic island, or a mountain top, and show identical nearest neighbour relationships to taxa in a quite separate area on the earth. The main features of global biogeography have been summarized by Croizat (1958) and represented as standard distribution tracks (Fig. 1.8). Croizat identified distinct trans-oceanic patterns linking the same terrestrial areas together over and over again, and showed that the generalized patterns linked together. Identifying sympatric distributions of distantly related taxa in similar areas which have nearest neighbour relationships in a similar disjunct area is often a first step in recognizing areas of endemism. Thus, we recognize that the Macaronesian element of the Canary Islands has nearest relatives on the west coast of Africa, the marsupials of south-east Australia have nearest relatives in west Australia, the carabid beetles

Table 1.2 A broad classification of major distribution patterns of seed plants (after Thorne 1972; Stott 1982)

I	Eurasian-North American
	1 Arctic
	1a Circum-Arctic
	1b Beringian Arctic
	1c Amphi-Atlantic-Arctic
	2 Boreal
	2a Circum-boreal
	2b Beringian-boreal
	2c Amphi-Atlantic-boreal
	3 Temperate
	3a Circum-north temperate
	3b North-south temperate
	3c Fragmentary-north-temperate
II	Amphi-Pacific tropical
III	Pantropical
IV	African-Eurasian (-Pacific)
	1 African-Mediterranean
	2 African-Eurasian
	3 African-Eurasian-Malesian
	4 African-Eurasian-Pacific
	5 African-Eurasian-Australasian
	6 Indian Ocean-Eurasian
V	Amphi-Indian Ocean
VI	Asian-Pacific
	1 Asian-Papuan
	2 Asian-Papuan-Melanesian
	3 Asian-Papuan-Pacific Basin
	4 Asian-Papuan-Australasian
VII	Pacific Ocean
VIII	Pacific-Indian-Atlantic Ocean
IX	American-African
X	North American-South American
XI	South American-Australasian
XII	Temperate South American-Asian
XIII	Circum-south temperate
XIV	Circum-Antarctic

of New Guinea have nearest relatives in north Australia, and so on. Examination of the ecological conditions of each species in one area of endemism does not really explain sympatry. For example, why do southern beech trees show broad distributions similar to chironomid midges when neither is necessarily dependent on the other? Is it that both have

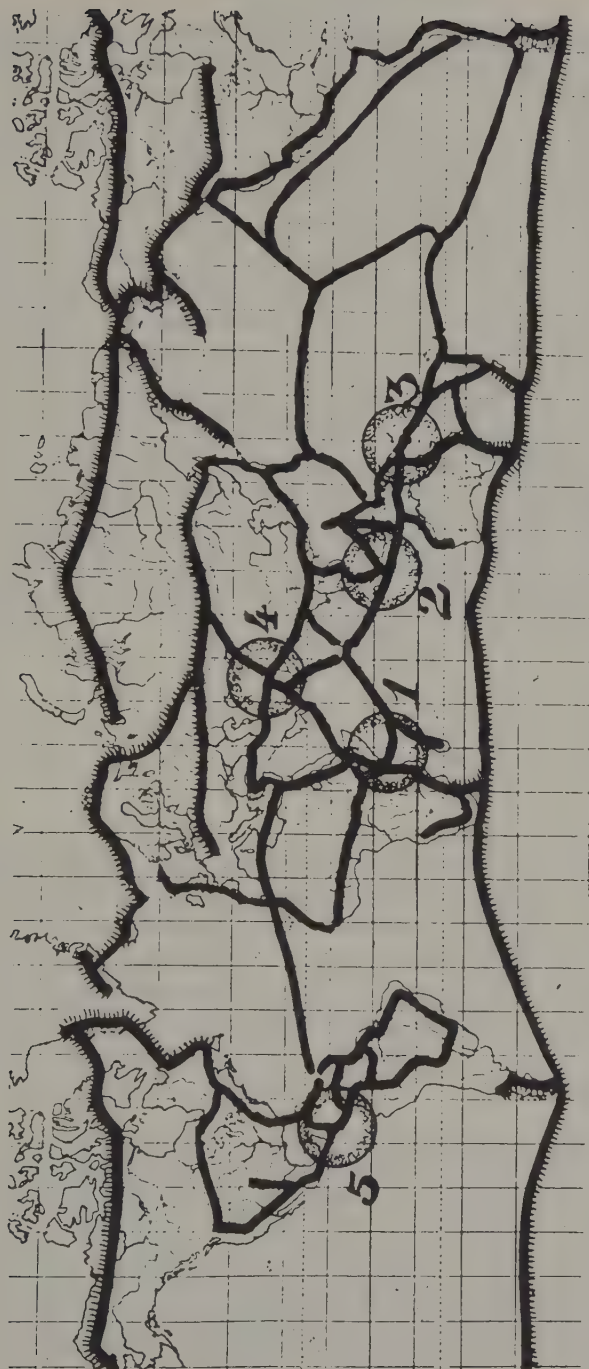


Fig. 1.8 The main features of global biogeography summarized by Croizat (1958, IIb: 1018, Fig. 259). The lines represent generalized tracks. Hatched lines represent 'boreal' and 'austral' tracks. The major biogeographic nodes are numbered 1-5. Note that the Americas are represented twice to indicate both trans-Pacific and trans-Atlantic connections.

independently become adapted to similar southern hemisphere habitats, or does the history of the biotas in which they occur provide a different answer?

Delimited areas of endemism are hypotheses about the units of biogeographic analysis. Taxa that delimit areas are the characters that define areas; relations between taxa in three or more areas are the characters or homologies that suggest relationships between those areas. Hypotheses about areas can be modified in the light of new data, much as the definition of terminal taxa in systematic analyses are revised with further research. The limits of at least one taxon boundary is the minimum requirement to identify an area for biogeographic analysis. Unless there are at least two taxa from different monophyletic groups occupying similar, and ideally identical, or at least partially overlapping areas, however, there is no pattern and no real expectation that there is a single, general historical explanation of the distribution (Axelius 1991; Platnick 1991; Harold and Mooi 1994). Areas of endemism are defined at a scale appropriate to the level of analysis of inclusive taxa, their hypothesized relationships, and their delimited distributions (Harold and Mooi 1994). Criteria proposed for recognizing areas of endemism are explained in greater detail in Chapter 2 (see Morrone 1994; Crisci and Morrone 1995).

1.3 HISTORY OF IDEAS

1.3.1 Origins

That every organism has a particular distribution pattern has concerned biologists for more than two centuries. Modern systematics is generally regarded to have started with the work of Carolus Linnaeus (1707–1778), the Swedish naturalist and early developer of a theory of hierarchical classification, and one of the earliest writers to interpret the distribution of organisms. Linnaeus believed that the earth was changing, with continents growing in size, and concluded that if this process had operated in the past:

... the continent in the first ages of the world lay immersed under the sea, except a single island in the midst of this immense ocean; where all animals lived commodiously, and all vegetables were produced in the greatest luxuriance . . .

Translated from Linnaeus 1781, p. 77, after Nelson and Platnick 1980

Linnaeus realized that organisms had various ecological requirements and suggested that the primordial island must have been in the tropics, and 'bore a very lofty mountain' inhabited at different altitudes by species with different ecologies. As new land emerged when the seas receded, organisms

migrated by various means to colonize those parts with suitably similar ecological conditions (Nelson and Platnick 1980). Within these comments are two important ideas: that species originate and disperse from a 'centre of origin', and that regularities in distribution are controlled by ecological conditions. Development and better expression of these ideas appears in Willdenow's *Grundriss der Krauterkunde* (1798), Part 7:

By history of plants is meant the influence of climate on vegetation, the changes which plants have probably undergone as a result of the revolutions which have taken place on our globe, their distribution over the earth's surface, their migrations, and, lastly, the provisions nature has made for their preservation.

Willdenow, after Wulff 1950

According to Wulff (1950), a number of questions were in Willdenow's mind—did the seas of today formerly occupy much greater areas? Indeed, was not the earth once almost entirely covered with water, from which projected mountain peaks, then the only habitats available for terrestrial organisms? As the seas receded, land area increased, and plants and animals dispersed from the initial habitats. Later, great geological climatic events such as hurricanes, earthquakes, and volcanoes destroyed life over huge areas. This is supported especially by the distribution of closely related endemics in widely separated areas:

Lands now separated by oceans may, in former epochs, have been united . . . Thus, the northern part of America may have been connected with Europe, New Netherlands (Australia) with the foothills of the Cape of Good Hope . . .

Willdenow, after Wulff 1950

This is a prophetic passage in that in addition to migrations, present-day disjunctions might be caused by the separation of formerly continuous biotas. Despite such a concise statement by Willdenow, it is generally regarded (e.g. Wulff 1950; Nelson 1978) that Humboldt is the founder of phytogeography and Buffon the founder of zoogeography. Buffon (1776) had already formulated the general principle that animal life was very different between different areas of the world, especially the mammal faunas of Africa and South America, when Humboldt and Bonpland (1805) expressed some remarkable ideas about the history of the earth:

. . . to come to a decision as to the existence in ancient times of a connection between neighbouring continents, geology bases itself on the analogous structure of coastlines, on the similarity of animals inhabiting them and on ocean surroundings. Plant geography furnishes most important material for this kind of research. It can, up to a certain point, determine the islands which, at one time united, have become separated from one another; it finds the separation of Africa and South America occurred before the development of living organisms. It is again this science that shows which plants are common to both eastern Asia and the coastlands of Mexico and California, and whether there are some which grow in all zones and at all altitudes. It is by the

aid of plant geography that we can go back with some certainty to the initial physical state of the globe. It is this science which can decide whether, after the recession of the waters to whose abundance and movements the calcareous rocks attest, the entire surface of the earth was covered simultaneously with diverse plants, or whether according to the ancient myths of various peoples, the globe, having regained its repose, first produced plants only in a single region from which the sea currents carried them progressively, during the course of centuries, into the more distant zones

Humboldt and Bonpland 1805, pp. 19–20, after Wulff 1950, p. 11

Humboldt and Bonpland were convinced that the history of organisms and the history of the earth go together, and the Linnaean idea that organisms originated in one area and migrated to others was ill-founded. Besides distribution as a key to the past, Humboldt and Bonpland also suggested that the examination of fossils would give not only clues about the migration of plants over the globe but also some clues as to what past climates would have been like:

... to solve the great problem as to the migration of plants, plant geography descends into the bowels of the earth: there it consults the ancient monuments which nature has left in the form of petrifications in the fossil wood and coal beds which constitute the burial places of the first vegetation of our planet . . .

Humboldt and Bonpland 1805, p. 22 after Wulff 1950, p. 11

Thus, by the turn of the nineteenth century, three sets of ideas existed in biogeography:

- that organisms could originate from one (or more) ‘centres of origin’ and migrate to other parts of the globe;
- that changes in the world itself—earth history—could explain differing distribution patterns; and
- that different habitats and climates could determine the perceived present-day pattern.

The principal point to emerge was the generality of Buffon’s original observation that different areas, especially the new and old world tropics, contain different species, which is true for all organisms, not just mammals.

1.3.2 Habitations

Together with acquisition of additional data on the distributions of particular organisms came advances in the classification of distributions as evidenced in the work of Candolle. He distinguished between two branches of plant geography—the equivalents of modern ecological and historical biogeography. Candolle (1820) discussed the influence of external elements, temperature, light, and humidity in determining ‘stations’, or habitats as

we call them today, and also different types of plant distributions in 'habitations' or areas.

Ecological biogeography is the study of stations; historical biogeography the study of habitations. Candolle thought confusion between the two aspects would undermine the development of either science. It was clear to Candolle that the factors which determined stations were quite different from those which determined habitations. He also noted that cosmopolitan species were exceptions to the general law of distribution—namely that different species occur in different habitations. He concluded that cosmopolitan species transcended habitation boundaries by dispersal and noted that plant seeds could be transported by the continual action of three causes—water, wind, and animals, including humans. This could explain why certain species occur in different continents. To account for particular distribution patterns Candolle deduced that all plants originated in a particular region.

Candolle's classification is shown in Table 1.3. The list is a good approximation of some areas of endemism that we recognize today. Of interest to us is the fact that Candolle's comparative studies of the regions allowed him to recognize endemic genera with many species occurring in one area and that certain genera occur in widely disjunct regions. As one explanation of disjunction and endemism, Candolle resurrected Willdenow's idea that

Table 1.3 Candolle's 20 botanical regions

1	Boreal Asia, Europe and America
2	Europe south of the boreal region and north of the Mediterranean
3	Siberia
4	The Mediterranean region
5	Eastern Europe to the Black and Caspian Seas
6	India
7	China, Indo-China and Japan
8	Australia
9	South Africa
10	East Africa
11	Tropical west Africa
12	Canary Islands
13	Northern United States
14	North-west coast of North America
15	The Antilles
16	Mexico
17	Tropical America
18	Chile
19	Southern Brazil and Argentina
20	Tierra del Fuego

mountains form barriers between regions and rejected the idea that they could be a 'centre of origin'. He did not suggest that mountains and continental break-up could cause the divisions between regions, because if that were the case one would expect the same species on either side of a mountain range. Instead, he criticized the immutability of species, inherent in theories of geographical botany at that time, and considered the origin of species to be due to external forces as yet unknown.

The important point to emerge from Candolle's work is that his regions were roughly equivalent to what are recognized today as areas of endemism, and a precise statement of Buffon's original observation. Subsequent studies in historical biogeography took two, divergent courses. On one hand, as evidenced particularly in the work of Forbes (1846), there was an interest in considering the history of earth and its biota together, whilst on the other, as in the work of Darwin, there was a separation of the two.

1.3.3 One history

As a starting point for his exposition on the history of the British fauna and flora, Forbes (1846) assumed the existence of 'specific centres' or 'certain geographical points from which the individuals of each species, originating from a single progenitor or two, began their geographical distribution'. As an explanation for particular distributions, duckweed in ponds, alpine herbs in mountains, and trees in forests, Forbes concluded that organisms are adapted to particular conditions and will migrate only into those places of which they are capable. Examining the interrelationships of the British flora, the various different elements, according to Forbes, could have only come about by the migration of species from continental areas prior to the separation of the British Isles from the mainland. Of interest to us is that Forbes arrived at his conclusions using the evidence that several similar or identical species in disjunct areas are best explained not by repeated dispersals but by one isolation event.

These ideas were developed further by the botanist Joseph Dalton Hooker who provided general explanations for the phytogeography of the whole earth—a transition from the study of small, separate geographic units to entire continents. Hooker's biogeographical studies ranged from the Galapagos to the floras of the southern hemisphere and the tropics. Hooker interpreted the distribution of organisms in a most plausible manner. Thus, the origin of organisms on oceanic islands, such as the Galapagos flora, could be explained as the result of the transport of its component species, especially the non-endemics, by transport on ocean currents, by wind, by birds, or by humans. The individual appearances of island taxa were due to later modifications under the influence of isolation. However, his best known contribution came later in his introduc-

tory essays to his *Botany of the Antarctic Voyage*. In volume II, the *Flora of New Zealand* (Hooker 1853), using Lyell's principle that each species can only have arisen at one point on the globe, Hooker reasoned that the widely disjunct islands of the Antarctic, with very similar floras, must have formed a single area—a land mass occupying a continent larger than that in the Antarctic ocean. In volume III (Hooker 1860), devoted to the flora of Australia and Tasmania, are two more sections of interest to us: 'On the general phenomena of distribution of plants in area' and 'On the general phenomena of the distribution of plants in time'. In the former, Hooker writes that the present distributions of plants can only be explained by past events, and to study them it is necessary to study past changes in climates and the distribution of dry land. In the latter, Hooker reviews palaeontological data to advance the proposition that changes in the earth's surface—lands replaced by sea, and valleys replaced by mountains—take place in a very short time relative to the ages of biological groups. Hooker thus provided a solution by stating that organisms and continents change through time—life and earth are intimately entwined. He thus favoured former land connections, such as between New Zealand and South America, to explain major biotic similarities between continents (see Grehan 1991).

1.3.4 Separate histories

By the middle of the nineteenth century it was becoming accepted that the earth and its biota changed with time and that a general theory of mutability of species was lacking. Darwin's *Origin of Species* appeared in 1859, but surprisingly, he separated his mechanism of evolution from biogeography. In fact, only Chapters 11 and 12 are devoted to biogeographical questions yet they greatly influenced later ideas on distribution. Darwin opens Chapter 12 with the statement:

In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be wholly accounted for by climatal and other physical conditions . . .

Darwin 1859, p. 346

Darwin responded to Candolle's 'origin of species problem' by saying that the similarities of the biotas in southern hemisphere lands and the similarities of the North and South American organisms were due not to changes in the earth's surface but to inheritance:

We see in these facts some deep organic bond, throughout space and time, over the same area of land and water, independently of physical conditions . . . The bond is simply inheritance . . .

Darwin 1859, p. 350

The difference between species, the unique characters of varieties and different species, according to Darwin, originate because each species is produced in one area, subsequently migrating from that area and changing by natural selection through time. Chapter 12 concludes with another profound statement:

The endurance of each species and group of species is continuous in time; . . . so in space, it certainly is the general rule that the area inhabited by a single species or by a group of species is continuous and the exceptions, which are not rare . . . be accounted for by former migrations under different circumstances, or through occasional means of transport, or by the species having become extinct in the intermediate tracts . . .

Darwin 1859, p. 409

Thus, Darwin proposed a method of biogeography that could account for all possible distributions. The finding of similar species in the British Isles and in Europe was easy to comprehend, since until relatively recent time they formed a continuous land surface. At the same time, Buffon's observations of differences in the biotas of Africa and South America, despite similar habitats, is understandable, because they have been separated for a long time. For Darwin, however, the occasional existence of identical species separated by vast distances attests to great dispersal abilities (in the sense of range expansion, rather than other definitions of the term; see Myers and Giller 1988 for a fuller account of the problems surrounding this concept). The context used here is that Darwin criticized the geologist Lyell and the biogeographer Forbes also when he wrote:

Other authors have thus hypothetically bridged over every ocean and united almost every island with some mainland. If indeed the arguments used by Forbes are to be trusted, it must be admitted that scarcely a single island exists which has not recently been united to some continent. This view cuts the Gordian knot of the dispersal of the same species to the most distant points, and removes many a difficulty; but to the best of my judgement we are not authorised in admitting such enormous geographical changes within the period of existing species.

Darwin 1859, p. 357

In fact, Darwin allowed only certain types of earthly revolutions: 'great oscillations in the level of land and sea' and also 'existence of many islands, now buried beneath the sea, which may have served as halting places for plants and for many animals during their migration' (Darwin 1859, pp. 505–6). Thus, on the age of taxa Darwin had an opinion opposite to that of Hooker: taxonomic groups are younger than the places they inhabit. To prove the point that dispersal by seed propagules from parental plants must be the means by which plants migrate to oceanic islands, Darwin undertook a great many experiments on seed survival in sea water. The successful survivors he took as experimental proof of dispersal, which he applied as

the general mechanism. Darwin thought that millions of years of chance dispersals, especially to those islands newly forming from the sea bed, would be sufficient to stock them with raw materials for future evolution. In other words, dispersal and subsequent isolation created areas of endemism. Darwin differed from Candolle, Lyell, and Forbes, for whom dispersal accounted only for widespread or cosmopolitan species (Nelson 1978). With respect to the relative importance of dispersal, as distinct from the earth's physical features, to explain biogeography, Alfred Russel Wallace followed Darwin and focused on dispersal. His investigations were significant because to him the complex distribution of organisms over the earth was the outcome of both biological and 'physical' forces. To quote Wallace:

The biological causes are mainly of two kinds—firstly, the constant tendency of all organisms to increase in numbers and to occupy a wider area, and their various powers of dispersion and migration through which when unchecked, they are enabled to spread widely over the globe; and secondly, those laws of evolution and extinction which determine the manner in which groups of organisms arise and grow, reach their maximum, and then dwindle away, often breaking up into separate portions which may survive in remote regions.

Wallace 1880, pp. 531–2

Wallace also subscribed to geological forces which could isolate whole biotas and changes in climate which were the main causes of extinction.

The issue for both Darwin and Wallace and, indeed, for the subsequent Darwin–Wallace tradition dominant for the past 100 years, was that because dispersal occurred as migration, every taxonomic group had its own distributional history. Thus, for an area containing endemic species with nearest relatives elsewhere a special kind of 'isolating dispersal' is required to explain endemics. Dispersal by migration, once successfully achieved by a species, results in its isolation and subsequent differentiation into an endemic taxon (Nelson 1978). For Wallace there were two kinds of isolating dispersal: dispersal over a pre-existing barrier and then isolation, and dispersal of one species over a wide area followed by extinction of the intermediate populations to separate populations once forming a continuum. Despite philosophical shifts in geology, systematics, and biogeography, the Darwin–Wallace tradition has continued more or less unabated through this century (e.g. Raven and Axelrod 1972, 1974; Briggs 1984, 1995; Cox and Moore 1993). As Nelson (1978) put it, the concentration on a class of improbable dispersals as an explanation for different taxa occupying different areas of endemism results in the 'science of the rare, the mysterious and the miraculous'.

Thus, Darwin's work tended to focus on histories of specific organisms; to address the problem of similarities between different biotas he used an experimental approach to ascertain effective means of dispersal. Alternatively, Hooker was impressed by Darwin's experiments and, despite his

contribution that continents as well as organisms could change through time, left Hooker with a paradox; either migration of plants and animals, or former land-bridges, could both fully explain any given situation so the choice of one over the other did not really provide one solution in preference to another (Grehan 1988, 1991). Consequently, the conceptual differences facing Darwin and Hooker involving two alternatives—vicariance (equivalent to land-bridges and continental drift) and dispersal through migration over a world of fixed geological features—was a false apposition. A radical new approach was required. There was a need for a theory and method to overcome the static geography of vicariance versus dispersal framework, an approach that could determine the units of biogeography, and some equivalent of homology to determine the relationships between different areas of the globe.

1.3.5 Sclater's regions

The missing element from nineteenth century biogeography was the notion of the interrelationships of the areas in which individual groups of organisms occur. Sclater (1858) proposed a classification of the world based on the distributions of birds. Wallace (1876) considered that these regions, which he called 'realms', might apply not only to birds but to animals in general and they have been used ever since (Fig. 1.9). For Wallace, realms expressed the similarities of animal taxa in various areas of the world. Thus, an animal in Britain would generally be more like another animal from somewhere in the Palaearctic realm than from, say, the Ethiopian realm. These realms, although rather an abstract concept, did give some measure of the areas of the world that have each had a long and independent biotic evolution with overall taxonomic differences between the biotas of the different areas (Ross 1974). In other words, a vague assessment of the degree of relatedness of patterns on a global scale.

Most interestingly, Sclater realized the problem of relationship when he said:

Little or no attention is given to the fact that two or more of these geographical divisions have much closer relations to each other than to any third.

Sclater 1858, p. 131

Sclater was not particularly satisfied with his six 'realms' but suggested that more systematic work would eventually allow us to arrive at the correct primary divisions of the globe. There have been many attempts to refine Sclater's classification of very large spatial units into smaller ones. Today there are a number of qualitative and quantitative systems that try to divide the existing global biota into more refined units but there is no universal

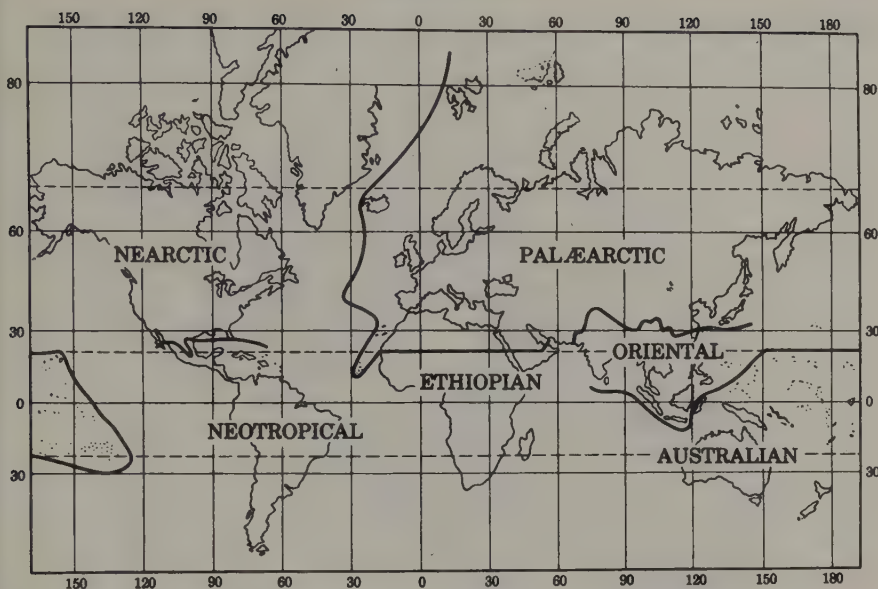


Fig. 1.9 Traditional faunal regions (or realms) (after Sclater and Wallace, as modified by Ross 1950).

agreement as to how this should be undertaken (compare for example the maps of Udvardy 1975, at a global scale with those of Simpson 1982 in Grehan 1989, for New Zealand in Figs 1.10 and 1.11; see Hengeveld 1990 for review). Woodward (1856) made one of the first attempts to delimit explicit quantitative biogeographical units, proposing that for two areas to be different from each other at least 50 per cent of their species should be different. In 1908, Jaccard developed a precise similarity coefficient; since then, a number of clustering algorithms and analyses based on overall similarities between biotas assessed as shared species have been published (e.g. Sokal and Sneath 1963; Holloway and Jardine 1968; van Balgooy 1971; Sneath and Sokal 1973; Pielou 1984). Curiously, though, despite Sclater stating the precise ingredient for a method to find general relationships of biogeographical patterns, it remained another 60 or 70 years or more before the necessary approaches for ascertaining homologies could be fully realized.

We can conclude, then, that by the end of the eighteenth century it was known that:

- species occur in different areas;
- areas apply to both animals and plants;
- there are biogeographical regions or areas of endemism; and
- the areas are related to one another.



Fig. 1.10 Biogeographic realms as determined by Udvardy (1975).



Fig. 1.11 Outline map of ecological regions and districts in the Protected Natural Areas Programme classification in New Zealand (after Simpson 1982 in Grehan 1989).

Also, there had been many attempts to produce classifications of areas largely through counting similarities and differences between species distribution. There was another tradition building, however. The main question for many biogeographers in the twentieth century became: How does one determine the 'centre of origin' for different taxa using the processes of evolution and dispersal as causal agents for distribution?

1.4 CENTRES OF ORIGIN

When considering the history of a biota in a particular area, some biogeographers refer to distributional change on a geographical scale as almost entirely due to some form of range extension by jump dispersal with subsequent evolutionary change associated with disjunction (see Myers and Giller 1988). Taxa are conceived as having colonized beyond their initial ranges over a period of time, through processes brought about by exogenous agents such as prevailing winds, marine currents, or even animal transport. The dispersal biogeographer asks: Where did the group originate, and when and how did it come to occupy the place in which it lives today? For each question there are many possible answers and the choice depends entirely on what the author interprets as evidence.

Some of the more coherent attempts to identify centres of origin in phytogeography were made by Adams (1902), Willis (1922), Cain (1944), and Wulff (1950). Adams wrote that such criteria should be regarded solely as:

. . . convenient classes of evidence to which we may turn for suggestions and proof as to the origin and dispersal of organisms . . . It should be clearly emphasized that it is the convergence of evidence from many criteria which must be the final test in the determination of origins.

Retrospective methods make various assumptions as guides to determine the 'centre of origin'; it may be the area in which the group of organisms displays the greatest diversity, or number of species, the area in which the most primitive forms occur, the area occupied by the most phylogenetically advanced or primitive members, or where the oldest fossils occur. Cain listed 13 criteria for recognition of centres of origin (Table 1.4). Each criterion may give a markedly different result. For example, Humphries (1981) discussed 11 different theories for the origin of the southern beeches, *Nothofagus* (Nothofagaceae), involving almost every continent; the favoured choices for a centre of origin have been North America, Europe, south-east Asia, New Caledonia, and somewhere between Queensland, Antarctica, and New Zealand. This list is by no means exhaustive.

As Forey (1981) noted, a theory about the 'centre of origin' may deter-

Table 1.4 Cain's (1944) criteria for determining 'centres of origin'

(a)	The location of the greatest variety of forms of the taxon
(b)	The location of the area of greatest dominance and density of distribution
(c)	The location of the most primitive forms
(d)	The location of the area exhibiting the maximum physical development of individuals
(e)	The location of the area of maximum ecological productivity of the taxon
(f)	Continuity and convergence in the lines of dispersal
(g)	The location of least dependence on a restricted habitat
(h)	The identification of continuity and directness of individual variations or modifications radiating from a 'centre of origin' along the highways of dispersal
(i)	The area of origin indicated by natural geographical affinities
(j)	The direction of origin indicated by the annual migration routes of animals, especially birds
(k)	The region of origin indicated by seasonal appearance or general phenology
(l)	An increase in the number of dominant genes towards the 'centre of origin'
(m)	The concentricity of progressive equiformal areas

mine or be dependent upon a theory of a presumed dispersal route. The route from the centre to the present-day whereabouts is usually made by reference to a variety of influencing facts: the occurrence of fossils, the age of the fossils, the past climate of the earth, and so on. For example, to account for the resemblances in the North American and Asian palaearctic mammal faunas, Simpson (1962) suggested that there were four major exchanges between North America and Eurasia. The Bering Strait was the favoured highway and because of the cold climatic regimes at the presumed time of migration, only temperate rather than tropical mammals were to have moved. Besides fossils, so-called living fossils have also been used as evidence for origins of dispersal routes. Takhtajan (1969) asked the question: 'Can we in fact find out what part of the world was the cradle of the flowering plants?' His answer: 'It was evidently a region in which they experienced a long period of evolution during which the principal families and many genera were differentiated, and it may also have been their centre of origin; in any case it was probably not very far from their birthplace.'

Some authors sought a 'cradle' in high latitudes with an Arctic or Antarctic origin (Heer 1868) whilst others sought in the lower latitudes of the tropics or subtropics (e.g. Diels 1908; Wulff 1950; Smith 1970; Thorne 1972; Stebbins 1974). Bailey (1949) offered some advice: 'Look

west, young man, towards the remnant of Gondwanaland'. According to Takhtajan (1969), the striking restriction of 'primitive' angiosperms to the islands and borders of the Pacific ocean indicates that: 'It is here, in eastern and south-eastern Asia, Australasia and Melanesia that the cradle of the angiosperms must be sought.' For Takhtajan, the conclusion rests on the occurrence and preponderance of primitive forms; that is, those plants believed to possess primitive characters. Thus, he believed it was largely from the western Pacific that colonization of the world by angiosperms has taken place since the Cretaceous because the 'oldest' angiosperm fossils are to be found in the Barremian of the Cretaceous (see Hughes *et al.* 1979) and the greatest number of 'living fossils' reside around the Pacific. A third, but less specific place of origin is one with a mesophytic climate, as suggested by Stebbins:

The most progressive vascular plants of the Jurassic period were probably the angiosperms which, if they existed today would be classified as belonging to or related to the Magnoliales. A logical assumption, therefore, is that the pioneer, ecotonal and mosaic habitats found in semiarid, sub-tropical mountainous regions were at that time occupied by the original ancestral Magnoliales and Dilleniales.

Stebbins 1974, p. 205

Raven and Axelrod (1974, p. 635) are a little more precise as to the exact location of such a place and suggest that west Gondwanaland might be the 'primary area of evolution' for 'many orders of angiosperms, and perhaps the earliest angiosperms themselves'.

By what means the organisms migrate from the 'centre of origin' is a newer question and is related to the identification of hurdles which inhibit movement. Simpson (1953) recognized three types of barriers to migration by degree of faunal similarity between areas:

- corridors—obvious heavy load migration routes—indicated by high similarity;
- filters—for example, big deserts, water gaps, and narrow strips of land, indicated by low similarity allowing only light load traverses; and
- 'sweepstake' routes—the truly formidable barriers such as major oceans—which only allow the rare chance crossings.

Sweepstake routes are usually invoked to explain 'unbalanced biotas'—depauperate flora and fauna showing peculiar or ecologically unbalanced admixtures of organisms. The principles of dispersal biogeography have remained consistent over the last century. Because dispersal hypotheses reside in a narrative framework they are irrefutable. Migrations have simply been modified to fit in with new views of earth history (Peake 1982).

Dispersal hypotheses do not attempt to provide a general theory of earth history but rather individual case histories for each taxonomic group. Consequently, dispersal biogeography is a discipline divorced from earth history and invariably couched in the possible processes which could give rise to modern distribution patterns. Dispersal biogeography is an *ad hoc* discipline since it always requires external causes to explain the patterns (Croizat *et al.* 1974; Platnick and Nelson 1978; Nelson and Platnick 1981; Patterson 1981a; Nelson 1982, 1983). Consequently, dispersal hypotheses can never let us discover the history of the earth.

1.5 PANBIOGEOGRAPHY

Although much twentieth century biogeography interpreted distribution patterns using dispersalist scenarios, best shown by the writings of Matthew (1915), Cain (1944), Simpson (1953, 1965), and Darlington (1957, 1965), radical alternative theories to 'centres of origin' have appeared (e.g. Wulff 1950; Croizat 1952, 1958, 1961, 1964; see also Craw 1978, 1979, 1982, 1983, 1985; Melville 1981; Grehan 1991; Craw *et al.* 1999). Croizat (1952, 1958, 1961, 1964) undertook the laborious task of effectively re-examining Sclater's problem—which areas of endemism are more closely related to one another in terms of other areas, and by providing a solution to Hooker's paradox—by developing a general method of identifying biogeographic homologies, by linking distributions of related taxa in 'track' analysis. The general approach he described as 'panbiogeography'—the biogeography of all organisms throughout the world. Despite the massive output in his lifetime, Croizat's view of earth history and evolution may be reduced to two general principles: tectonic change, not dispersal, is the causal explanation for different areas containing different species; the main biogeographical regions for terrestrial organisms correspond not directly to composite or hybrid modern continents, unlike Candolle's habitations and Wallace's realms, but rather to modern ocean basins (Nelson 1978, p. 295). His interpretation was a break from the Darwin–Wallace tradition, and instead a development from the ideas of Buffon, Candolle, Hooker, and Wulff. Croizat thought that tectonic change was all important, for it is that process which allows 'form-making' or recognizable taxa in particular areas which give us the present-day distinctive forms of animal and plant life. A direct corollary is that the distributional areas are causally inter-related, and the basis of that relationship is subject to investigation because all species and their definable distribution areas must ultimately exhibit a global pattern of interrelationships (Nelson 1978, p. 296). As distinct from dispersalism, which separates geological history and distribution, Croizat (1958) brought the two together. His view on the role of dispersal is novel.

For him, 'dispersal' is the causal factor to explain related species occupying different areas. Instead of a species migrating from one area to another and fragmenting the range, disjunctions could also be seen as a result of tectonic change and they represent the ranges of former taxa.

For us, the best description of Croizat's method is in *Space, Time, Form: The Biological Synthesis* (1964), but see also Craw (1982). For example, Croizat (1964, p. 7) considered the breaks in distribution of taxa occurring in North and South America, particularly the repetitious gaps or disjunctions between Mexico and Peru, Mexico and Bolivia, Mexico and Chile. The localities of groups of related taxa are connected together by a line or track which is indicated on the map as a graph of geographic distribution. In the example (see Fig. 1.12) the track indicates that a certain taxon occurs in western North America, Hawaii, and Bolivia, the last two areas of endemism being sharply separated from the first. In other words, the track places the coordinates of a group in space and according to Croizat (1964, p. 7) opens the way to an enquiry into factors of time and form. As we shall see in Chapter 2, cladistic biogeography has re-ordered these dependencies because considerations of form are an essential prerequisite to any enquiry into time and space, thus making the track a distribution graph of a monophyletic group.

The distribution of one taxon may coincide with the distributions (tracks) of other taxa. Coincident distributions involving several unrelated species or monophyletic groups (coincident individual tracks) conform to reality and are components of a general biotic distribution, or a generalized track (Fig. 1.13). The distribution of most species and of most monophyletic taxa coincides with part or all of that of some other species or group, and many therefore occupy one part or all of a generalized track. The most generalized tracks include the largest number of, and the most biologically diverse groups of organisms, both fossil and Recent, and are therefore the most thoroughly confirmed (Croizat *et al.* 1974, p. 265). As Croizat (1964, p. 7) noted, if a given individual track recurs in group after group of different organisms to yield generalized tracks, these coincident distributions become statistically and geographically highly significant and require general explanations.

When disjunct monophyletic taxa occur repeatedly in the same areas of endemism, the pattern is likely to be due to one of a series of historical events that created that pattern of disjunction. In other words, generalized tracks represent the present-day patterns of ancestral biotas. By determining what major types of coincident patterns occur on the globe today, the number of individual tracks composing each generalized track, and the variety of organisms incorporated in each track (Croizat 1964, p. 21), allow ancestral biotas to be recognized (Croizat *et al.* 1974).

Once tracks had been identified they can be linked together to

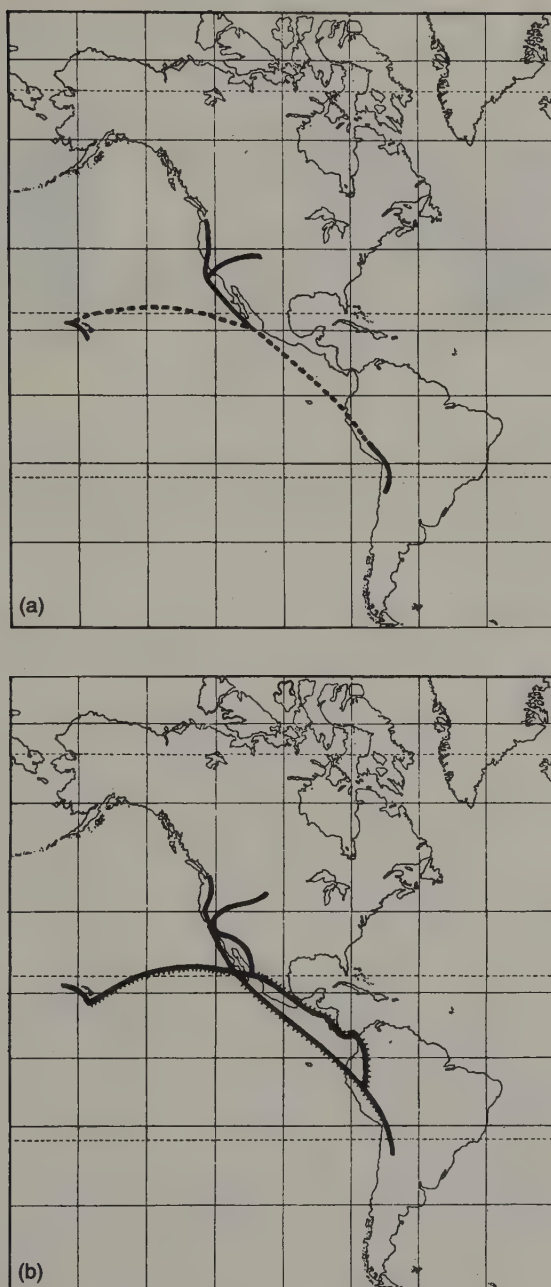


Fig. 1.12 Generalized tracks (after Croizat 1964, Figs 1 and 2): (a) geographic distribution; (b) generalized track.



Fig. 1.13 Concept of oceanic baselines for differentiating tracks drawn as minimal spanning trees (hypothetical example after Craw and Page 1988).

understand biogeographic patterns at broader scales. Much of Croizat's analyses involved identifying the points (nodes) where two or more tracks intersect (Craw 1989a). At the intercontinental scale, for example, Croizat (1958) identified five major biogeographic nodes, centres or gates; the African Gate (1), Tenasserim-Flores/Sumbawa (2), Neo-Caledonia (3), Altai (4), and nuclear Central America (5) (Fig. 1.8). Croizat recognized that modern continents are invariably complex in their biogeographical relationships. Characteristically, many disjunct patterns spanned ocean bottoms, to the point that the oceans have been characterized as the natural biogeographic regions and the continents represent the land areas around the periphery (Fig. 1.14; see Craw and Page 1988; Parenti 1991).

Of the better known examples of generalized tracks with a trans-Pacific baseline, we illustrate Hooker's example of the southern hemisphere areas of South America, Tasmania, Australia, and New Zealand (Fig. 1.15). Different groups of organisms occur in these four southern areas and exhibit nearly identical patterns of disjunction. Thus, the coincident distributions of freshwater fishes, earthworms, molluscs, birds, mammals, insects, mosses, and flowering plants (Croizat 1952; Good 1964, 1974; Brundin 1966; Croizat *et al.* 1974; Craw 1979, 1982; Humphries 1981; Patterson 1981a) pose a general problem concerning the original distribution and subsequent history of a pan-austral biota. To what does the evidence add up?

The ancestral biota might once have been geographically widespread and later subdivided in relation to disruptive geological events, or each group might have had a 'centre of origin' elsewhere and come to occupy the

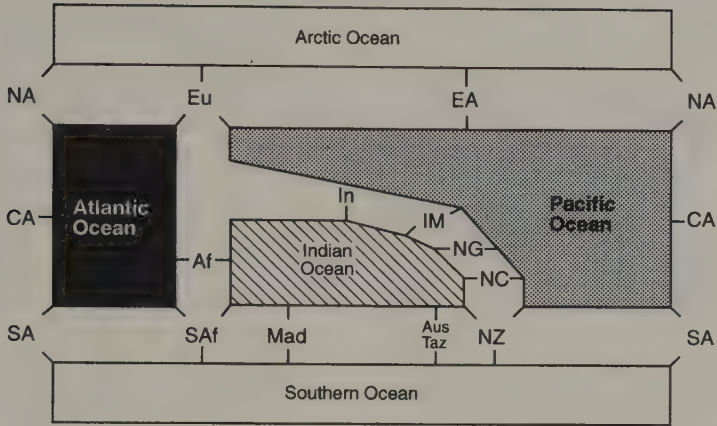


Fig. 1.14 Panbiogeographic classification of the globe with ocean basins representing natural biogeographic regions and major land areas located at the boundaries of the regions (after Craw and Page 1988). Definitions: NA, North America; Eu, Europe; EA, East Asia; CA, Central America; Af, Africa; SAf, South Africa; Mad, Madagascar; Aus, Australis; Tas, Tasmania; SA, South America; NZ, New Zealand; In, India; IM, Indo-Malaysia; NG, New Guinea; NC, New Caledonia.

present-day distributions by migration and colonization. The problem is how one assesses such patterns. Can it really be possible that *Nothofagus* seeds or thousands of tiny midges are carried by long distance dispersal agents to other lands thousands of miles away? Yet, so many identical tracks occur for many different groups. A generalized track is a constraining reference and it is more likely that the pattern is caused by a single event or a series of historical events to explain the repeated patterns.

Generalized tracks are not restricted to terrestrial examples but may also concern marine biotas that were once formerly continuous and have since subdivided. A spectacular example is the amphi-American marine biota separated by the isthmus of Panama, where several monophyletic groups exhibit an eastern Pacific–Caribbean track. The advantage of the track and the generalized track are that the coordinates in space are determined on the general relationship of taxonomic groups totally independent from geological considerations. The limitation of tracks, however, as we shall see in Chapter 2, is that they only connect the areas that are causally related without considering the pattern of relationships of the areas connected by the track (Fig. 1.16, after Croizat *et al.* 1974; Rosen 1976).

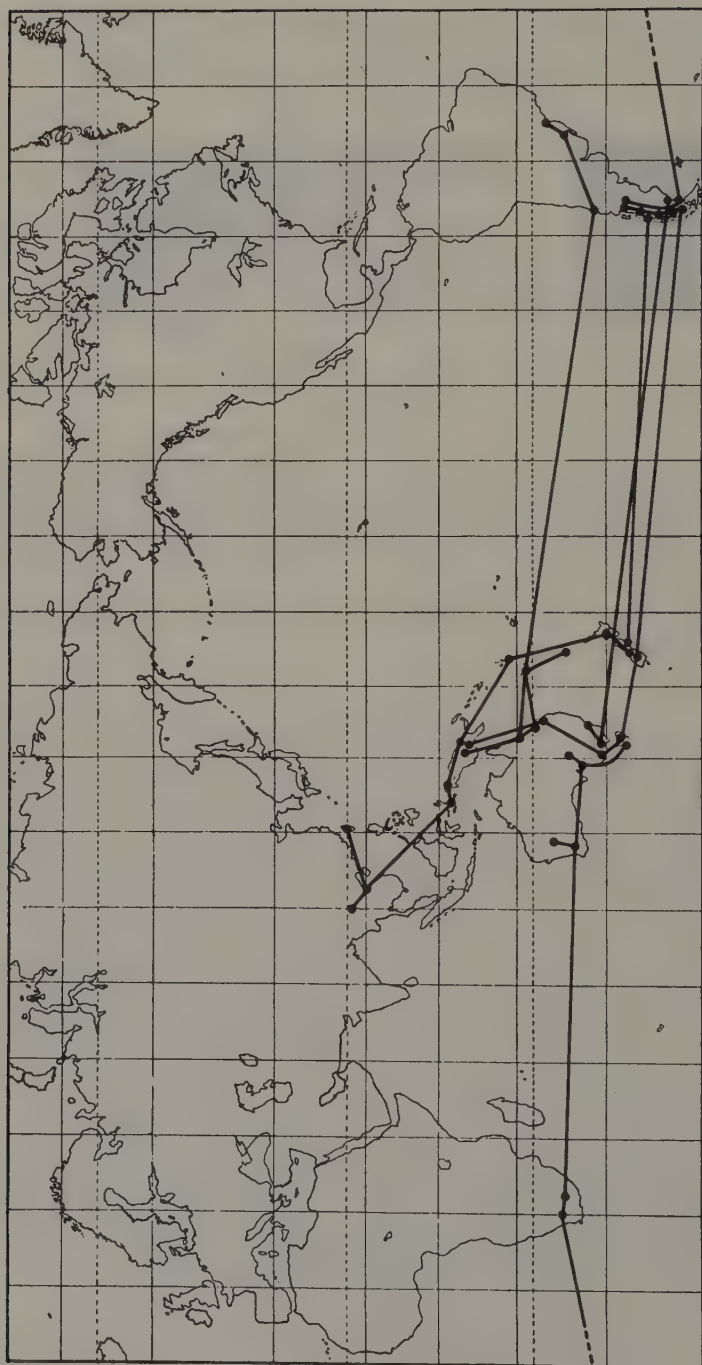


Fig. 1.15 Some generalized tracks for the southern hemisphere and south-east Asian tropics; chironomid midges, *Nothofagus*, Restionaceae, *Araucaria*, and *Libocedrus*.

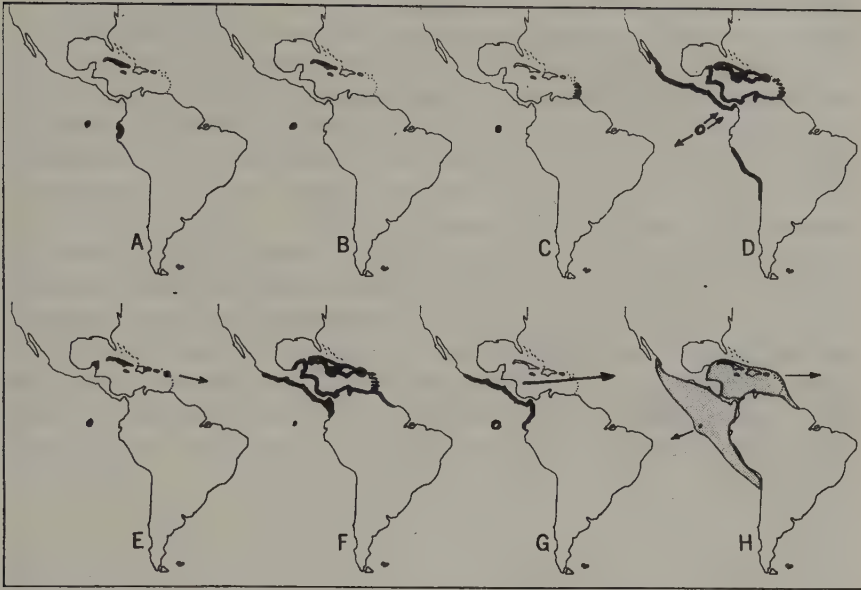


Fig. 1.16 Generalized tracks of monophyletic components of the eastern Pacific-Caribbean generalized track: (a) isopods of the genera *Jimenezia*, *Colombophiloscia*; (b) isopods of the genera *Troglomphoscia* and *Nesophiloscia*; (c) extinct rice rats of *Megalomys*; (d) brachyuran crabs; (e) atyid shrimps of *Typhlataya*; (f) several fish groups; (g) generalized distribution of stomatopod crustaceans; (h) generalized track for all groups in (a)-(g). (After Rosen 1976, Fig. 5, p. 441.)

1.6 CONCLUSIONS

Historical biogeography, from Linnaeus to Croizat, may be seen as a series of different propositions for the causes of present-day distribution patterns. For Buffon's patterns of allopatric distribution, Candolle suggested that earth history was all important. For Willdenow and Humboldt, former land-bridges explain disjunctions. For Wallace and many twentieth century workers such as Matthew, Cain, and Simpson, dispersal by Darwin's 'occasional means of transport' played a significant role which effectively immunized their efforts from criticism. The problem with all the solutions is that they lacked a testable definition of relationship. The global significance came with the work of Croizat. Panbiogeography removed the false dichotomy that biogeography was explanation of present-day distributions by dispersal versus vicariance arguments, but that dispersal needed to be understood in terms of biogeographic regions and biogeographic homologies. Despite claims made by supporters of the panbiogeographic

method, however, track analysis lacks rigour in determining what constitutes the raw data of biogeographic homologies and what precisely determines area relationships (see Seberg 1986, for example). Consequently, the concept of regions when classified using degrees of similarity is meaningless. Even generalized tracks, although they offer a solution to identifying areas of endemism, contain only generalized statements of the connections between areas. Until Hennig (1950, 1965, 1966) clarified the concept of relationship in systematics the question of relationship between areas of endemism similarly could not be understood. The lessons from history are clear. For biogeographical theories to be meaningful, falsifiable statements must be derivable from them at two different levels. First, what constitutes an area? Second, what are the relationships among those areas? Of the two classes of causal factors, dispersal and vicariance, which is the most meaningful for our hypothesis of earth history? The cladistic answers to these questions are outlined in Chapter 2.

2

Methodological developments

2.1 INTRODUCTION

Developments in the theory of continental drift and its general acceptance during the 1960s and 1970s confirmed the idea that disjunct biotic patterns and corresponding geological patterns are due to the same events in earth history. That the earth, including relative sizes and composition of land masses, constantly changes means that many, if not all, migration or dispersal solutions to biogeographic questions are wrong, or, at least, overstated. To us, a more realistic solution came when Brundin (1966) applied Hennig's (1950) definition of phylogenetic relationship to the problems of vicariant distribution of southern hemisphere chironomid midges. Ensuing developments in biogeographic theory brought Croizat's panbiogeography into the limelight. Fused with cladistics, this became cladistic biogeography. Cladistic biogeography is about understanding relationships of areas through discovery of biotic patterns. Systematic patterns became comparable and understandable for biogeography when expressed as area cladograms. Area cladograms—branching diagrams of areas—express relationships of areas as determined from phylogenetic classifications by substituting the name of a taxon for the area in which it occurs, and combining individual taxon cladograms into generalized area cladograms (Section 2.3). The methodology of cladistic biogeography is still developing and there are several methods we have omitted, such as 'parsimony analysis of endemism' (PAE) (see Rosen and Smith 1988; Crisci and Morrone 1995) which is not an historical method. The purpose of this chapter is to describe methodological developments more-or-less chronologically. Later, we show that different taxonomic groups may show the same pattern of area relationships and, therefore, that it is possible to make a general hypothesis about relationships of areas of endemism and of biotas. Corroborated hypotheses of this sort can be compared with similarly organized, but independent, information from geology.

2.2 CLADISTICS

Cladistics is a systematic method formulated by the German entomologist, Willi Hennig (1913–1976). The method is known also as phylogenetic systematics (from the English translation of Hennig's 1966 book), Hennigian systematics, or cladism. A comprehensive review of Hennig's ideas and initial responses to them is given by Dupuis (1978). Hennig's method is significant in that in describing a general method of phylogeny reconstruction, he provided a precise meaning of relationship which stimulated a new and vigorous period of systematic research. Books describing cladistic methods include those by Eldredge and Cracraft (1980), Nelson and Platnick (1981), Wiley (1981), Brooks and McLennan (1991), Wiley *et al.* (1991), Forey *et al.* (1992), Maddison and Maddison (1992), Quicke (1993), and Kitching *et al.* (1998). Hennig originally enunciated a method for reconstructing phylogenetic trees, but, in the late 1970s, it became subtly refined into a method with more general properties and a much wider application than perhaps originally intended. Similarly, cladistic biogeography has undergone a series of subtle changes that parallel those in phylogenetic systematic method. Therefore, we give an outline of phylogenetic systematics appealing to common ancestry for definition of monophyletic groups as originally advocated by Hennig (1966), since it is presented in this way by some authors (e.g. Eldredge and Cracraft 1980; Wiley 1981; Maddison and Maddison 1992; Quicke 1993), together with a description of so-called transformed cladistics which emphasizes that pattern analysis be restricted to empirical observations (e.g. Platnick 1979; Patterson 1980, 1982a,b; Nelson and Platnick 1981; Forey *et al.* 1992).

Darwin's (1859) theory of evolution by natural selection has two aspects: a pattern of relationships caused by evolution through common descent, and a mechanism of change by natural selection. This theory was intended to explain the natural hierarchy of animals and plants. Groups of daisies and sunflowers, or foxes and rats, belong to larger groups of flowering plants or mammals, and each belongs to even higher groups of land plants and tetrapods, all of which evolved from a single common ancestor (e.g. Fig. 2.1). Linnaeus and his successors recognized that organisms could be described as species and then be arranged into more inclusive natural groups, such as genera, families, and orders, each of which could be categorized by similarities. Linnaeus believed he was reconstructing the plan of Creation and that characters used to group genera and families were the essences corresponding to such a plan. Darwin's (1859) contribution was to suggest that the hierarchical relationship between genera and families were 'blood' relationships or kinships caused by descent from a common ancestor. His often cited dictum in the *Origin of Species* sum-

marized his view of relationships: 'our classifications will come to be, as far as they can be so made, genealogies; and will then truly give what may be called the plan of creation.' Darwin's expectations have mostly failed to materialize because classifications are constructed for two purposes—to express phylogenetic relationships and to act as identification keys that summarize similarities, or dissimilarities, between different groups. As Patterson (1982a) pointed out, it has traditionally been understood that these two aims conflict because relationships based on common ancestry are almost invariably more complicated than relationships of similarity or differences on which keys are based (see Fig. 2.1). Cladistics is a refined method that offers a solution to the conflict by equating phylogeny and classification. Cladistics gives results of greater utility for biogeographical problems than do non-phylogenetic methods (such as overall similarity) which do not summarize phylogeny in classification schemes.

The importance of Hennig's method is his definition of phylogenetic relationship and his protocol for its recognition. Phylogenetic relationship can be demonstrated with a rooted, branching diagram, a cladogram (Fig. 2.2). Species B is hypothesized to be more closely related to species C than to another species A, since B and C have at least one common ancestor at time t_2 which is not ancestral to species A. Similarly, species A, B, and C form a monophyletic group because they have a common ancestor at time t_1 not shared by any other taxon, Z. The task of phylogenetic systematics is to identify monophyletic groups. According to Hennig, monophyletic groups could only be recognized by shared derived characters, which he called synapomorphies, inherited from the most recent common ancestor. Shared primitive characters (symplesiomorphies) inherited from a more remote common ancestor are irrelevant in reconstructing genealogies. For example, in Fig. 2.2 the relationship of B and C may be obscured by features inherited from an ancestor (at t_1). The bony spinal column and the ability to lay eggs of the duck-billed platypus are uninformative with respect to its relationship to other mammals because both characters (symplesiomorphies) occur in a much larger group, including lizards and birds. On the other hand, hair and mammary glands, for example, are shared derived characters (synapomorphies) unique to monotremes and other marsupial and placental mammals. Hennig called characters unique to a group 'autapomorphies'. Thus, he divided the concept of resemblance or character distribution into three sorts: autapomorphy, synapomorphy, and symplesiomorphy, which describe the distribution of any character among a set of taxa. Hair and mammary glands are autapomorphies when one is trying to discover the relationship of mammals to lizards and birds, symplesiomorphies when trying to discover the interrelationships of rats, sheep, and pigs, and synapomorphies when trying to discover the relationship of a duck-billed platypus to a rat and a bird.

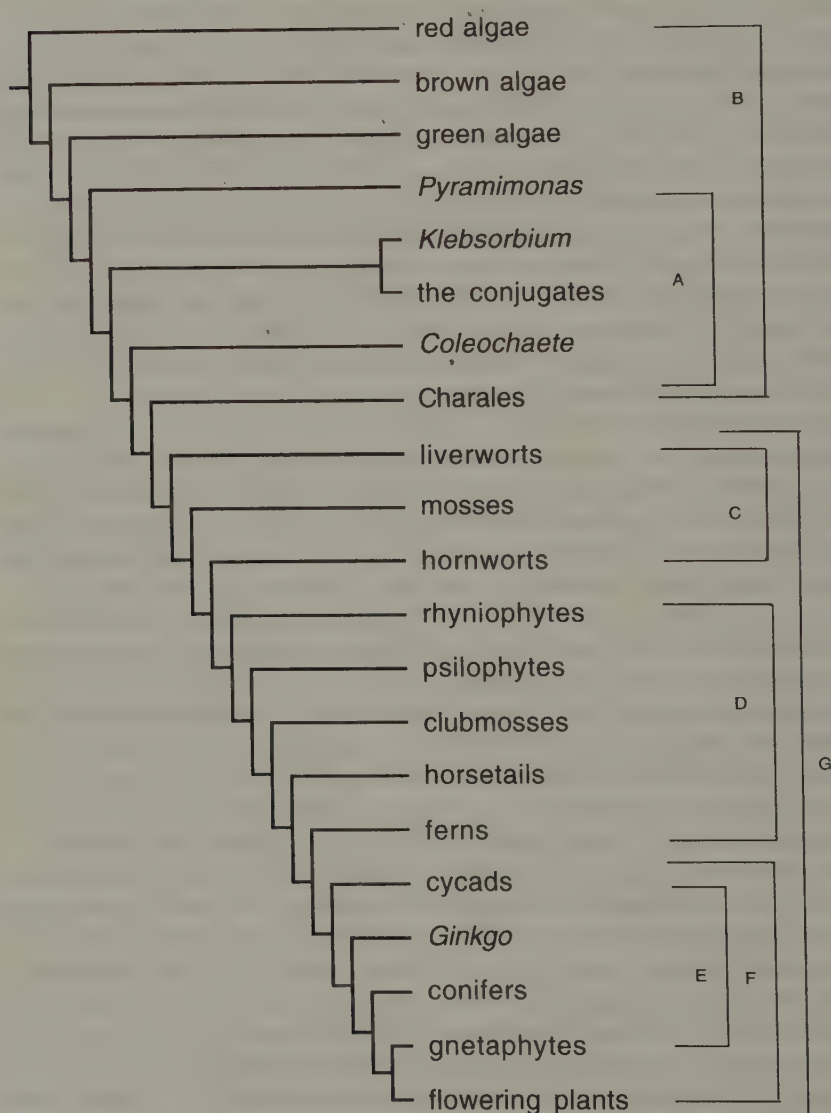


Fig. 2.1 Genealogies and traditional classifications in the land plants and their closest allies. Nodes represent taxa based on group-defining characters; only two taxonomic classes, the Embryobionta (G) and the seed plants (F), agree with the genealogy. Other classes (A–E) agree with some traditional groupings (after Parenti 1980; Bremer and Wanntorp 1981; Hill and Crane 1982). A, Charophyta; B, Algae; C, Bryophyta; D, Fern allies; E, Gymnospermae; F, Spermatophyta; G, Embryobionta.

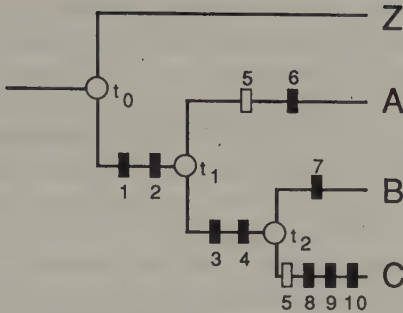


Fig. 2.2 A cladogram showing Hennig's (1966) definition of relationship. A, B, C, and Z represent Recent taxa; numbers represent 1–10 characters (character 5 in white boxes indicates a parallelism); t_0 , t_1 , t_2 are relative time intervals.

From concepts of character distribution, Hennig derived definitions for the three types of groups:

1. **Monophyletic groups:** based on shared resemblance derived from a common ancestor. In Fig. 2.2 the group ABC based on characters 1 and 2, and the group BC based on characters 3 and 4 are monophyletic. Vertebrates based on backbones, mammals based on hair, and viviparous mammals based on live birth are all examples of monophyletic groups.
2. **Paraphyletic groups:** that is, those that do not contain all the descendants of a common ancestor. A paraphyletic group is one remaining after one or more parts of a larger monophyletic group are separated from it because those members removed share many derived characters. Thus, in Fig. 2.2 if taxon C was put in a group of its own, because it has three times as many unique characters (8, 9, and 10) as either A or B, each with one unique character (6 and 7 respectively); then group AB is paraphyletic. AB is a group without a single defining character and may be recognized only by the absence of characters 8, 9, and 10. Classic examples include the Gymnospermae or the Algae amongst plants (Fig. 2.1) and Reptilia or Invertebrata amongst animals. There is no uniquely derived character that diagnoses any of these groups.
3. **Polyphyletic groups:** based on resemblance due to convergent or independently derived characters (e.g. character 5), not inferred to have occurred in the common ancestor; a group containing bats and birds based on a character stated as 'possession of wings' is one example (AC: Fig. 2.2).

Hennig's work was to infer phylogenetic relationships of various dipteran taxa, and his method was set in an evolutionary framework. His definitions of relationship, monophyly, synapomorphy, and symplesiomorphy are based on a notion of relative recency of common ancestry and transformation of characters during evolution. For Hennig, cladograms were phylogenetic trees with nodes, or branching points, denoting divisions of ancestral species and a time axis implied from the most inclusive node to the terminal taxa (Fig. 2.2). It is possible, however, to view cladograms in a more generalized framework—with a relative timescale and the nodes representing shared derived characters (synapomorphies) without the notion of a particular pattern of ancestry; the cladogram is the pattern of character distributions in the natural hierarchy. In a phylogenetic tree, the nodes are ancestors, the branch points are speciation events, and the lines actual lineages of descent with modification (Platnick 1979; Patterson 1982a,b). By contrast, a cladogram is a general summary of empirical evidence; of organisms and their characters consistent with a variety of phylogenetic trees. The cladogram (Fig. 2.3a), if viewed as a phylogenetic tree, specifies that species A, B, and C are all alive today, that the two hypothetical ancestors X and Y are now extinct, and that speciation was strictly dichotomous. The next five trees (Fig. 2.3b–f) are all equally consistent with four characters (1–4) but give other interpretations for the precise course of history. The cladogram (Fig. 2.3g) can thus be interpreted as a summary of a general pattern without any one particular evolutionary history or phylogeny specified.

More recently, Nelson and Ladiges (1991a–d) and Nelson and Platnick (1991) have developed yet another method, three-item statements analysis. As indicated above (Fig. 2.2), the fundamental problem to be resolved is the relationship among three taxa. Given three taxa, two may be more closely related to each other than either is to a third. Synapomorphic characters are the empirical units. Three-item statements analysis converts character distributions into all possible three-taxon statements as an expression of three-taxon relationships. Any systematic data set for more than three taxa (4, 5, n) can be transformed into another data set of three-taxon statements which can then be analysed to produce a result that Nelson and Platnick claim has greater resolution for all of the taxa than that inferred from the original data set.

The cladistic method demands that for groups to be monophyletic, they must be characterized by synapomorphies (equals homologies; Patterson 1982b). Many evolutionary taxonomists believe that a serious disadvantage of cladistics is that it does not weight evolutionary divergence, especially in classifications. As an example, consider the relationships of the flowering plants with other land plant groups, such as *Welwitschia*, *Ephedra*, and *Gnetum*, the conifers and cycads (see Parenti 1980; Hill and Crane 1982;

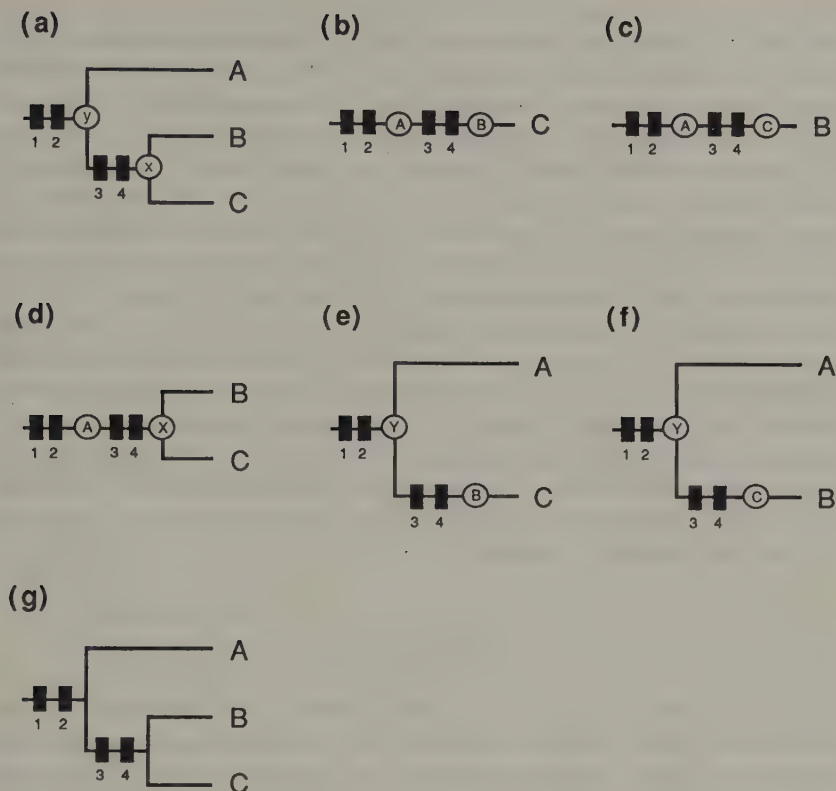


Fig. 2.3 Cladograms and phylogenetic trees: (a)–(f) represent six phylogenetic trees consistent with the cladogram in (g) defined on the basis of four characters (1–4).

Doyle and Donoghue 1986; Donoghue and Doyle 1989; Fig. 2.1). The angiosperms are grouped together because they have several synapomorphic characters, and the remaining taxa are classified as the gymnosperms. Hence, Gymnospermae is not a group by cladistic diagnosis, but by default. A classification based on such reasoning disagrees with a cladogram based on character analysis. If there is any criterion by which to judge a classification it is by parsimony, agreement with the greatest number of characters at hand. The best independent test of a cladogram on a given set of characters is whether an independent set of characters gives a similar cladogram; for example, DNA sequences and cytological data compared with morphological data.

Homologous characters are the only available clues to relationship and these allow us only to make general statements about group membership,

not specific statements about direct ancestry. Shared characters do not allow us to distinguish between two different interpretations of ancestry and so other criteria must be introduced. Fossils are used for interpretations of ancestry, especially when certain fossils appear earlier in the fossil record than others. Even with the best stratigraphic sequences, however, the characters of fossils must be interpreted in the same way as those of Recent taxa. Further, fossils are invariably incomplete and only interpretable by comparison with Recent taxa. Palaeontologists who claim to name a particular ancestor for a particular taxon, name instead ancestral groups—the Pro-gymnospermopsida being ancestral to Gymnospermae—with the idea that, if found, the actual ancestor would belong to that group. Extinct ancestral groups are paraphyletic artefacts if they cannot be identified by homologous characters, but only by ‘absences’, and there are no limits to their formation. Statements like ‘Gymnosperms evolved from the Pro-gymnospermopsida’ (see Beck 1976) seem absurd because one non-group could not have evolved from another. Cladistics allows us to discard the contention that fossils are required to reconstruct the phylogenetic or distributional history of a group.

2.3 CLADISTICS AND BIOGEOGRAPHY

Among the earliest applications of cladistics to biogeography were attempts by Hennig (1966) and others to use cladograms in relation to geographical distribution patterns to clarify monophyly. Hennig (1966) reasoned that there is a recognizable, close relationship between a species and the space it occupies. The ‘chorological’ method considered groups to be monophyletic if support from synapomorphies and the shapes of the cladogram topologies followed clear dispersal patterns from ‘centres of origin’ or exhibited sequential vicariance patterns. It appears that rather than saying that species and their areas or spaces evolve together, he assumed that dispersal patterns could either be unique for each taxonomic group and that each group has an independent history, or that vicariance events could explain the shape of the cladograms.

The best applications of Hennig’s biogeographic method are found in Brundin (1966, 1972a,b, 1981, 1988) for chironomid midges and also Ross (1974) for caddis-flies (Section 2.3.1). Although Hennig, Brundin, and Ross brought greater precision to biogeography by superimposing areas on to phylogenies and inferring the fewest dispersals for each group, their method relied on the *ad hoc* assumption that groups have ‘centres of origin’ from which members dispersed. A breakthrough in the application of cladistic reasoning to biogeography came, in our view, with the efforts of biogeographers such as Nelson, Platnick, and Rosen in their interpreta-

tions of Croizat. Instead of a 'vacuum' theory of biogeography, whereby certain areas were originally devoid of taxa later to be colonized from other source areas, there was proposed an equally plausible alternative. Disjunct distributions could come about by vicariance events because their ancestors occurred in the areas where Recent taxa occur today; the taxa evolved in place (Croizat *et al.* 1974). In other words, dispersal models explain disjunctions by dispersal across pre-existing barriers, vicariance models explain disjunctions by the appearance of barriers fragmenting ancestral species ranges. What became particularly clear was the important idea that distributional data alone are insufficient to resolve decisively whether dispersal or vicariance was the cause of a disjunct distribution pattern. Therefore, when faced with a particular distribution, as Platnick and Nelson (1978) argued, one should not worry initially about its cause, but first about whether or not it conforms to a general pattern of relationships shown by other groups of taxa endemic to the areas occupied. Thus, as in cladistics where a three-taxon statement is the basic unit for expressing relationships—a cladogram indicating that two taxa are more closely related to each other than either is to a third—in biogeography, a three-area statement is the most basic unit for expressing area relationships—a cladogram indicating that two areas are more closely related to each other than either is to a third. The generality of an area cladogram can be assessed by comparison with those of other taxonomic groups endemic to the relevant areas. Corroboration of one pattern by another is equivalent to making a general statement that the biotas share a history. To complete the analogy with systematics, we may ask, what is 'area homology' in biogeography? It is corroboration of a general hypothesis about the relationships of three areas of endemism.

Initial applications of the method (e.g. Rosen 1976) encountered incongruence and unresolved statements in the general area cladograms (Section 2.3.2). Theoretically, it should be possible to connect every area of endemism into one general statement of area relationships. Our perception of the world is less than perfect for a variety of reasons—extinction, dispersal of widespread taxa, and restricted distributions of taxonomic groups.

2.3.1 The progression rule

Central to Hennig's (1966) method to find a 'centre of origin' for a group of taxa from a particular cladogram was the idea that phylogenetically primitive members of a monophyletic group will, by definition, be found near that centre. Within a continuous range of species of a monophyletic group it was plausible that a transformation series of characters would run parallel with progression in space, such that the youngest members would

be on the geographic periphery of a group. An example is given by Ross (1950) for the *Wormaldia kisoensis* complex of caddis-flies. The geographical distribution of the nine species, eight species in the western Pacific from north-western Borneo in the south and Japan in the north, and one species in the Smoky mountains of eastern North America, is shown in Fig. 2.4. The cladogram of phylogenetic relationships is shown in Fig. 2.5. Ross (1974) assumed that the base of the stem denotes the ancestor of the group. That the most derived species pair occurs in Japan and eastern North America led Ross to accept the dispersal hypothesis of origin of the group in the western Pacific and a single dispersal of one species across the Bering straits to North America.

Brundin's (1966, 1972a,b, 1981, 1988) classic studies showed that the southern temperate areas of South America, southern Africa, Tasmania, south-east Australia, and New Zealand are inhabited by 600 to 700 species of chironomid midges. Transantarctic relationships recur throughout the group, but we restrict our comments to the cold-water midges of the subfamily Diamesinae, which display a double extratropical distribution: two major groups present in both northern and southern hemisphere temperate areas but absent from the tropics. The largest, and most widespread, is the relatively generalized tribe Heptagyini, represented by 11

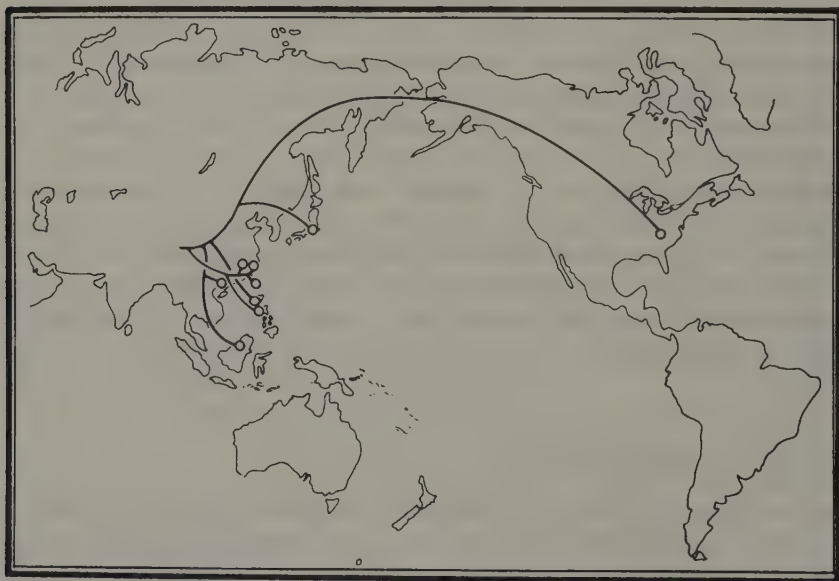


Fig. 2.4 Distribution and phylogeny of *Wormaldia*. The circle in Japan is *Wormaldia kisoensis*, that in eastern North America *Wormaldia mohri* (from Ross 1974, p. 217).

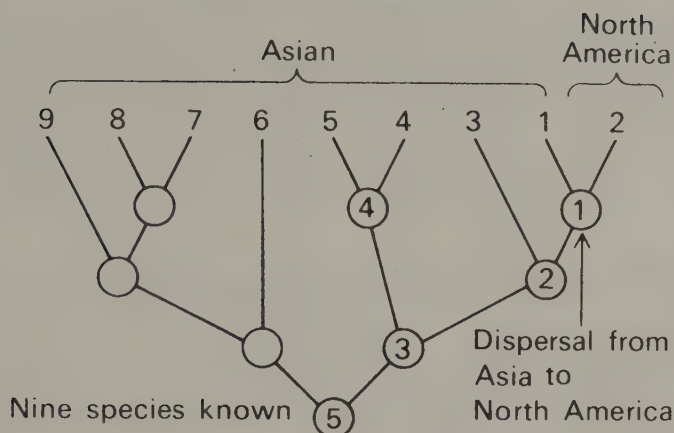


Fig. 2.5 Cladogram for the nine species of *Wormaldia* (see Fig. 2.4) (from Ross 1974, p. 216).

species in Andean South America, two species in south-eastern Australia, and five species in New Zealand. Its sister group is the relatively apomorphic monotypic New Zealand tribe Lobodiamesini. There are a total of 25 terminal taxa in the southern hemisphere areas of South America, New Zealand, Australia, and South Africa, and three groups in Laurasia (Fig. 2.6). The monotypic genus *Heptagyia* occurs in South America; *Paraheptagyia* has five South American species. According to Brundin, the south-eastern Australian subgroup of two species is a younger offshoot of the older South American group, including *Heptagyia*. Brundin considers the Australian taxa to have dispersed from Patagonia or east Antarctica at stem 6 by the end of the Palaeocene, because they share derived characters and because there is no evidence that the stem species (indicated by 1, 2, and 4) ever occurred in Australia. The other stem (2a) includes *Reissia* with three species in South America, *Limaya* with two species in South America, and *Maoridiamesa* with five species in New Zealand. Brundin (1981) considers that because *Maoridiamesa* is on a different stem from the Australian *Paraheptagyia* group, plate tectonic theory for an early separation of New Zealand from western Antarctica in the Upper Cretaceous is supported. That *Maoridiamesa* is a comparatively younger, derived offshoot of an older group in South America is, according to Brundin, evidence of long distance dispersal from South America via west Antarctica to New Zealand of stem species 4a, rather than of a vicariance event. In effect, Brundin supports the notion that *Maoridiamesa* group is younger than the areas in which it occurs.

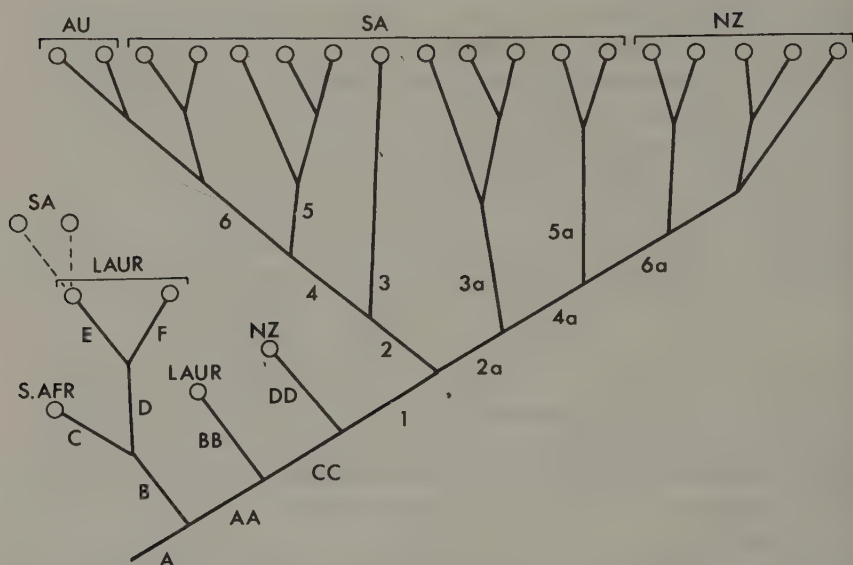


Fig. 2.6 Partial reconstruction and area cladogram of the subfamily Diamesinae (Diptera; Chironomidae). 1, Heptagyini; 3, *Heptagyia*; 4, *Paraheptagyia*; 3a, *Reissia*; 5a, *Limaya*; 6a, *Maoridiamesa*; A, Diamesinae; C, Harrisonini; E, Diamesini; F, Protanypodini; BB, Boreoheptagyini; DD, Lobodiamesini (from Brundin 1981, Fig. 3.7, p. 119).

There are more recent applications of the progression rule. Optimization of areas on a single cladogram to infer a centre of origin or dispersal is one implementation of the progression rule (viz. Liebherr 1989; Bremer 1992, 1995; Winterbottom and McLennan 1993; Ronquist 1994, 1995; Enghoff 1996). For example, Lundberg (1993) used optimization and fossil evidence to propose that some fish taxa are older and some are younger than the timing of a proposed split between South America and Africa. He concluded that trans-tropical Atlantic vicariant distributions of different taxa may have different causes. Lack of sufficiently old fossil representatives of cyprinodontiform killifishes and cichlids convinced him that dispersal across the Atlantic must have played a significant role in the distribution of these two widespread taxa. Because the New World (South American) distribution of killifishes is more general, he proposed dispersal from South America to Africa; because the African cichlids are primitive to New World (South American) cichlids, he proposed dispersal of cichlids from Africa to South America.

Interpreting cladograms as phylogenetic trees often requires making *ad hoc* assumptions not fully justified by the characters on which they are based. Furthermore, interpreting individual cladograms as having individual

histories leads to certain conceptual difficulties. One crucial difficulty is the repetition of distribution patterns. If we have distantly related taxonomic groups repeating a pattern of distribution among continents, it is improbable that each taxon has a unique dispersal history. To us, the most logical and simplest conclusion would be to suggest that at one time, the continents were in contact and that the present-day pattern is due to the break-up of a formerly continuous ancestral biota.

2.3.2 Vicariance biogeography—Croizat's (1952, 1958, 1964) methods and Rosen's (1976) method

Rosen set out to apply Croizat's method to Caribbean biogeography. The application has special significance because it was the first concise exposition of panbiogeography with cladistic hypotheses added; the groups analysed are all monophyletic rather than either monophyletic or paraphyletic, as in many of Croizat's examples. Craw (1983, 1989b) describes Croizat's (1958, 1964, 1982) panbiogeographic method as analytical biogeography because analysis of geographic distribution requires the equivalent of character analysis in systematics to determine what aspects of geographic distributions of taxa are 'homologous'. The concept of 'homology' to a panbiogeographer is phenetic and, therefore, not the same as homology to a phylogenetic systematist (see Mayden 1992).

For spatial analysis, there are four main components to Croizat's (1958, 1982) panbiogeographic method: tracks, baselines, main massings and biogeographic nodes. Tracks identify the spatio-temporal coordinates of a distribution of a species, genus, or family by lines drawn on a map that connect disjunct localities between the constituent taxa. A track is not synonymous with a distribution but instead connects localities and their spatial coordinates. Areas of high diversity, or centres of diversity, constitute main massings and were used to put direction on to particular tracks. Tracks are orientated such that they span the principal disjunction—often an ocean bottom or wide expanse of land. A suite of individual tracks for different groups of organisms showing similar distribution patterns are called generalized or standard tracks (Croizat 1961; Craw 1983). Time is correlated with differentiation among taxa. Croizat did not explain the pattern as being due to migration in an ecological, vicariant, or geological framework, but as dispersal, a change of locations or spatio-temporal coordinates, and a change in physical characters (form-making) (Grehan 1991). Although Croizat (1952, 1958) was never explicit about how he made tracks, Page (1987, 1990a) and Craw (1989b) described tracks as connecting distribution records using minimum spanning graphs. Heads (1990) showed that biogeographic nodes could be characterized by the presence of endemics, absence of groups found elsewhere, diverse

phylogenetic and geographic affinities, and phylogenetic and geographic limits of taxa. Page (1987) equated the biogeographic nodes with points of high connectivity on minimum spanning graphs, but they have also been considered as areas of conjunction between close proximity of tracks with different baselines, or at the ends of tracks, when two or more come into close contact with each other. Orientation of tracks to particular geographic sectors is accomplished by determining the baseline. The baseline thus provides the homology for disjunct distributions, in turn suggesting the relationships between the different areas occupied by component taxa.

Rosen (1976) recognized four generalized tracks for the Caribbean region: a North American–Caribbean track and a South American–Caribbean track, both mainly terrestrial; and an eastern Pacific–Caribbean track and an eastern Atlantic–Caribbean track, both mainly marine (Fig. 2.7). His sources of distributional data include plants, amphibians, reptiles, birds, mammals, and fish. The problem was to determine what these tracks

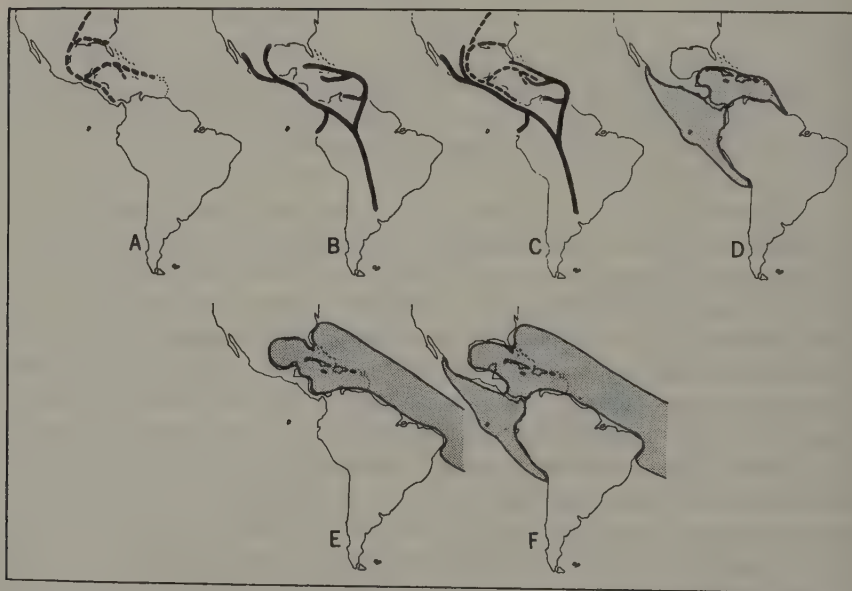


Fig. 2.7 Summary of transcontinental and transoceanic generalized tracks. (a) North American–Caribbean track; (b) South American–Caribbean track; (c) overlapping of North and South American–Caribbean tracks enclosing the Caribbean sea; (d) eastern Pacific–Caribbean track, the transoceanic track hypothesized to be youngest depicted here; (e) eastern Atlantic–western Atlantic track, a track of intermediate age; (f) eastern Pacific–eastern Atlantic track, hypothesized to be the oldest transoceanic track depicted here (from Rosen 1976, Fig. 6, p. 444).

mean in terms of distributional history. Rosen suggested that the four generalized tracks may be interpreted either as a result of four separate dispersal routes into the Caribbean or as vicariance events that subdivided widespread, ancestral marine and terrestrial biotas into smaller units. The first interpretation demands that dispersal was remarkably coordinated for taxa with such vastly different dispersal capabilities as, for example, birds, plants, and amphibians. The vicariance interpretation required geological events that isolated the eastern and western Atlantic, and the eastern Pacific from the Caribbean, followed by intermingling of North and South American biotas in middle America.

Rosen (1976) regarded dispersal hypotheses as untestable because they appeal to individual explanations: 'Thus, dispersal theories, if they attempt to deal at all with distributions in a rigorous way, are rather complicated and incorporate a major unexplained ingredient—namely the coordinated movements via active migration and chance dispersal of countless organisms of vastly different biological properties' (Rosen 1976, p. 445). Vicariance hypotheses, on the other hand, can be tested in two different ways: either by adding additional individual tracks, or by comparing the biogeographical hypothesis with a geological one. In the first test, new tracks will either be congruent or incongruent with the generalized track. The test is difficult to apply because incongruent tracks, assuming the taxonomy to be correct, can also be interpreted in one of two ways: as belonging to different generalized tracks or as dispersal events. Rosen pursued the second type of test in detail and found close agreement between the four-track model and Malfait and Dinkelman's (1972) account of Caribbean history.

The sequence of events for Rosen's general hypothesis, combining biogeography and geology, follows (after Patterson 1981a):

- (1) development of a later Jurassic proto-Antillean archipelago linking North and South America, colonized by dispersal from both continents and allowing limited dispersal of each continental biota to the other land mass;
- (2) displacement of the proto-Antilles to the east, as Pacific sea floor intruded between North and South America (the archipelago would have carried a mixed and now isolated North and South American biota, and the eastern Pacific marine biota would not disperse into the Caribbean);
- (3) development of an epicontinental seaway that isolated eastern and western North America;
- (4) development of a new lower central American archipelago that partially isolated the Caribbean from the eastern Pacific and was again populated by dispersal from north and south, allowing a second phase of dispersal between the North and South American biotas.

One flaw with this conclusion is its combination of vicariance and dispersal to explain tracks in light of geological theory. The striking concordance between biology and geology is compelling. As a method it is not new since classic dispersalist hypotheses (e.g. those of Wallace 1876; Matthew 1918; Darlington 1965) were also found to be concordant with geological hypotheses. As Patterson (1981a, p. 455) noted, recent accounts of Caribbean and eastern Pacific geology, especially tectonic sequences, are in disagreement with Malfait and Dinkelman's theory (e.g. Sykes *et al.* 1982). But, even if the geological hypothesis fades away, it does not falsify Rosen's biological data. The generalized tracks of monophyletic groups still stand and require explanation. There is another problem, however. Can a track be refuted in the same way as can a cladogram? Since a track merely connects a set of areas defined by a monophyletic group, is the track a meaningful way to express relationship in the same sense as does a cladogram? To some, generalized tracks are only a crude statistical measure of similarity between disjunct biotas (Ball 1976). Therefore, to make a comparison with systematics, tracks are analogous to measures of overall similarity in phenetics (Patterson 1981a). But, if monophyletic groups are used to formulate generalized tracks, the latter cannot be the same as similarity measures in phenetics because 'absence' data are disregarded. The question remains—are tracks measures of commonality or a measure of hierarchical relationship? Craw (1982) noted that Croizat (1952, 1958) invariably joined more than two areas together for reasons that were more than phenetic: 'In point of fact these diagrams (tracks) contain a natural concept of biogeographic regions . . . ' (Craw 1982, p. 306). Since a track is recognized on the connections of related taxa between disjunct areas, tracks represent generalizations in geography that may be analogous to cladograms in systematics. Tracks as used by Croizat (1952, 1958, 1964), although usually monophyletic, are not necessarily so. Since they are not hierarchical, but minimal spanning graphs connecting nearest neighbours, they show a more general resolution of geographical patterns than do cladograms. They not only indicate relationships of areas, they show especially the composite nature of existing areas, as do incongruent cladograms.

To improve the level of resolution it seems that what is required is the same type of information in geology and biogeography as that used in cladistics. In other words, to make satisfactory comparisons between organisms and areas it is necessary to have cladograms of areas that can be compared with taxonomic cladograms—a technique more rigorous than track analysis.

2.3.3 Cladistic biogeography—the method of Platnick and Nelson (1978)

A solution to a definition of area relationship came from the method of cladistic biogeography proposed by Platnick and Nelson (1978), which was applied to real examples by Rosen (1978, 1979). The method combined Hennigian cladistics with Croizat's panbiogeographic method by constructing cladograms of individual taxonomic groups that occupy the same areas. General area cladograms could be derived by adding the individual cladograms together to give statements about biotas.

Platnick and Nelson (1978) began their paper by asking the question 'Why are taxa distributed where they are today?' They gave two possible answers: either taxa evolved where they live today, or they evolved elsewhere and dispersed into that area. The difference between vicariance and dispersal lies in the relationship between the age of a taxon and the age of the barriers limiting the area. Vicariance predicts that taxa in two (or more) areas and the barriers between them are the same age; whereas dispersal always predicts that the barrier predates the taxa. Consider the American ivory nut palms (*Phytelephas*) which occur in lowland rainforest on both sides of the Andean mountains. A possible explanation for their present-day distribution is that the Andean mountain chain was formed during the Tertiary and subsequent separation of a widespread biota led to species differences on the east and west sides. That is, the ancestor of the present-day species was older than the barrier but the separation into two areas is the same age and due to the formation of the barrier. Dispersal interpretations are thus not easy to test because they are necessarily proposed separately for each group of organisms. In fact, many biogeographers believe that each group has its own dispersal history and the groups, therefore, are not comparable (e.g. Koopman 1981). Vicariance hypotheses can be tested by other taxonomic groups, fossil or Recent, that occur in the same areas under examination and inferred to have been affected by the same barriers.

The method of analysis involves first finding monophyletic groups with taxa occurring in at least three or more similar areas. Cladograms are proposed for each group of organisms. The names of the taxa at the terminal tips of the cladograms are replaced by the names of the areas in which each taxon occurs. The sum of the areas on one cladogram is equivalent to a track or ancestral area. The sums of similar areas on several cladograms are equivalent to generalized tracks. To obtain a cladogram of a biota, the individual cladograms are added together. For example, consider three areas of endemism, southern South America, Australia, and New Zealand, in which occur a genus of freshwater fishes with species A, B, and C, and a genus of flowering trees with species X, Y, and Z (Fig. 2.8a). The characters of each group are analysed and cladograms produced (Fig.

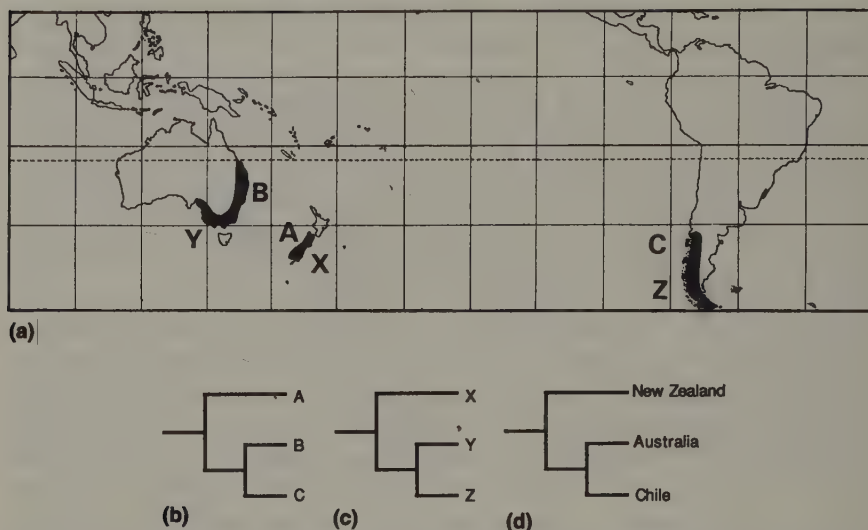


Fig. 2.8 (a) Hypothetical distribution of two groups—fishes (A, B, C) and flowering trees (X, Y, Z). (b, c) Cladograms for each group. (d) Area cladogram common to both groups.

2.8b,c). The area of each taxon is then substituted on the cladogram and yields identical area cladograms (Fig. 2.8d). The area cladograms are compared; they are congruent. The hypothesis for the three areas in this example is that Australia and southern South America are more closely related to each other than either is to New Zealand.

The success with which we find congruence in vicariant disjunct distribution patterns in nature depends upon the frequency with which common factors affect the evolution and distribution of two or more groups of organisms. To find congruent patterns, Rosen (1978) deleted unique, unresolved, or incongruent components from cladograms. Consider six areas of endemism—Australia, New Zealand, southern South America, New Guinea, Madagascar, and Africa—and the two monophyletic groups of fishes (A–D) and flowering trees (W–Z; Fig. 2.9a–c). The area cladograms (Fig. 2.9d,e) are not completely congruent since the fishes have a widespread species in South Africa and New Zealand and endemics in South America, Australia, and New Guinea. The flowering trees, by contrast, have one endemic species in each of Madagascar, New Zealand, Australia, and Papua New Guinea, but not in South America. By deleting the unique areas, South Africa, Madagascar, and South America, from both area cladograms, we produce one possible reduced area cladogram showing a common three-area pattern with New Zealand sister to Australia and New Guinea for both groups of organisms (Fig. 2.9f). Since Rosen's (1978)

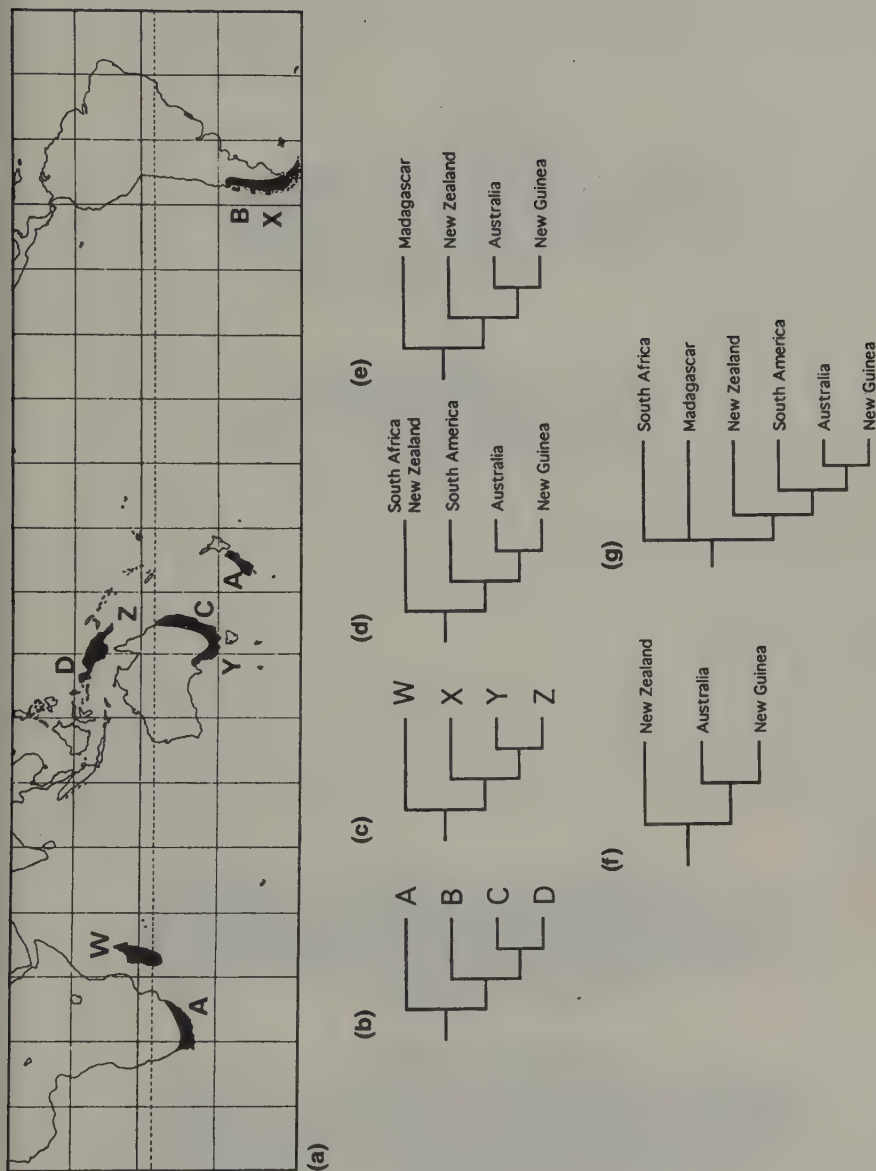


Fig. 2.9 (a) Hypothetical distribution of two groups—fishes (A–D) and flowering trees (W–Z) in the southern hemisphere. (b,c) Cladograms for each group. (d,e) Area cladograms for each group. (f) Reduced area cladogram. (g) Combinable components consensus tree of the cladograms in d and e.

analysis, there have been improvements in methods for combining data and cladograms (see Page 1989a, 1993a). Unique areas cannot cause conflict and unresolved areas cannot disagree. In a consensus tree, South Africa and Madagascar form a basal polytomy with a resolved group comprising New Zealand, South America, Australia, and New Guinea (Fig. 2.9g).

2.3.3.1 Poeciliid fish in Middle America—Rosen's example (1978, 1979)

During the past decade or so, application of cladistic biogeography has been dynamic (e.g. Hovenkamp 1987; Myers and Giller 1988; Page 1989a,b; Brooks and McLennan 1991; Ladiges *et al.* 1991; Morrone and Carpenter 1995), new methods have been proposed (Wiley 1987; Nelson and Ladiges 1991a–d, 1996), and implementation of existing methods improved (Page 1989a, 1993a). To recognize a pattern of area relationships, or 'area homology', phylogenetic analyses of at least two independent groups distributed in a similar set of three or more areas must be available. Rosen's analysis of poeciliid fish in Middle America was the first practical example of applying the Platnick and Nelson (1978) method to real organisms. Today, Rosen's data are still exemplary as almost every method and implementation has been tested with them, and his results remain the standard against which cladistic and vicariance biogeographic hypotheses of the Caribbean are judged (Savage 1982; Page and Lydeard 1994; Lydeard *et al.* 1995).

Poeciliids include a group of live-bearing or viviparous killifishes, distinguished by their unique modifications for internal fertilization and embryo retention (see Rosen 1978; Wiley 1980, 1981; Parenti 1981a). Rosen (1978, 1979) examined two distantly related Middle American poeciliid genera, *Heterandria* (Fig. 2.10) and *Xiphophorus* (Fig. 2.11). Both have



Fig. 2.10 *Heterandria cataractae* Rosen. (a) Female; (b) Male. (From Rosen 1979, Fig. 12.)

their closest relatives elsewhere, and each has a monophyletic subgroup inhabiting the same general areas in southern tropical Mexico, south to eastern Honduras in *Xiphophorus*, and further south to eastern Nicaragua in *Heterandria* (Fig. 2.12).



Fig. 2.11 *Xiphophorus cortezi* Rosen. (a) Female; (b) Male. (From Rosen 1979, Fig. 39.)

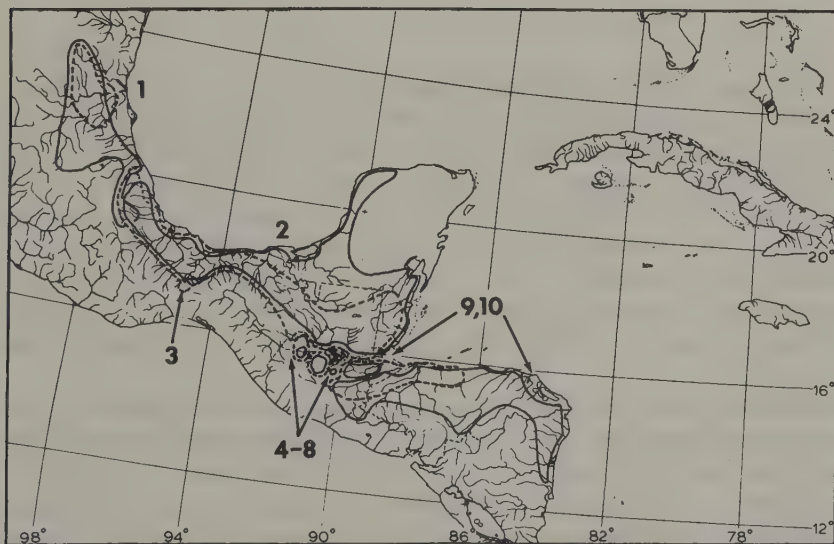


Fig. 2.12 Comparison of the distribution of the species of *Xiphophorus* (broken line) and *Heterandria* (full line) in middle America. Numbers refer to areas defined by the occurrence of taxa. See text for explanation. (From Rosen 1979, Fig. 45.)

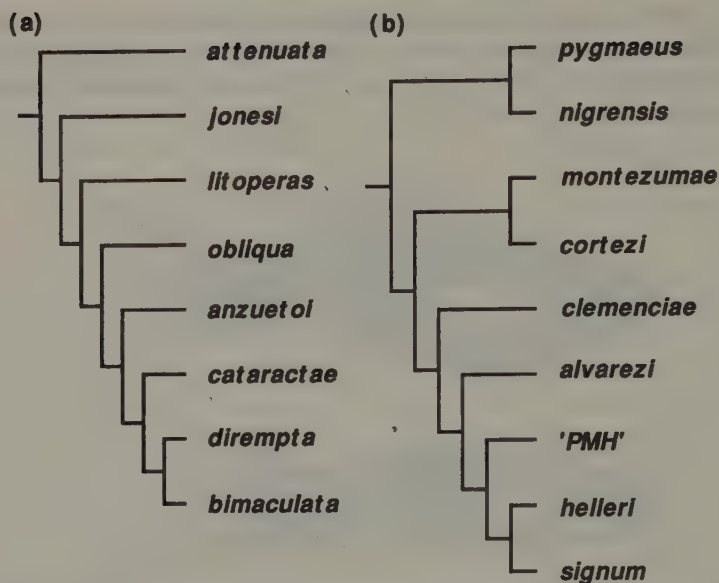


Fig. 2.13 Species cladograms for (a) *Heterandria*; (b) *Xiphophorus*. (After Rosen, 1979, Figs 48 and 49, pp. 371, 372.)

Cladograms for the two genera are given in Fig. 2.13. The cladograms for both genera are converted into area cladograms by substituting the name of the area inhabited by each species (Fig. 2.14). Next, simplified cladograms are produced using only one term for each area (Fig. 2.15). A reduced area cladogram common to both groups is then produced by deleting the unique information from each cladogram (Fig. 2.16). Rosen (1978) considered area 11 to be an area of intergradation or hybridization between two species in each genus. The common pattern is then inferred to reflect the history shared by *Xiphophorus* and *Heterandria*.

Rosen (1978, 1979) used reduced area cladograms to generate a biogeographical hypothesis for *Xiphophorus* and *Heterandria* because the individual cladograms were incongruent for certain areas. Cladistic biogeography would be simple if all groups of organisms were each represented by one, and only one, taxon in each of the smallest identifiable areas of endemism, but this is not true. Unique components in individual cladograms occur for a variety of reasons: failure of a population to divide in response to the formation of a natural barrier, dispersal from one area to another, and extinction in one or more areas, and so on. One problem with

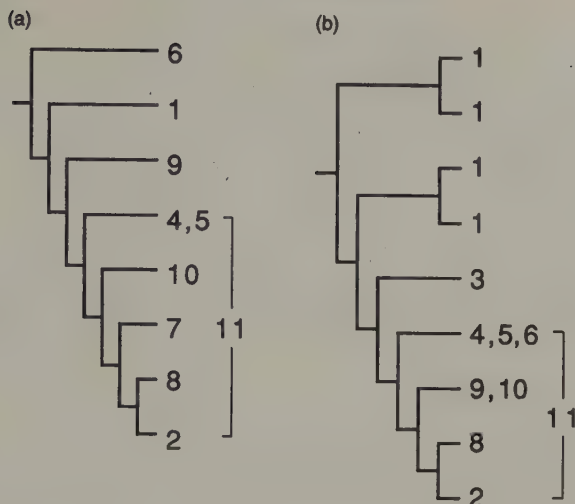


Fig. 2.14 Area cladograms for (a) *Heterandria* and (b) *Xiphophorus* including area components only once (after Rosen 1979, Figs 48 and 49, pp. 371, 372).



Fig. 2.15 Simplified area cladograms for (a) *Heterandria* and (b) *Xiphophorus* including area components only once (after Rosen 1979, Figs 48 and 49, pp. 371, 372).

Rosen's reduced area cladograms is that relevant information has been deleted from them. By deleting the incongruent elements of different patterns one may be 'fixing' the result. At least three solutions to this problem have been suggested; we describe them below.

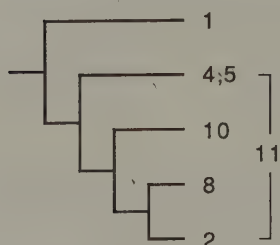


Fig. 2.16 Reduced area cladogram showing area components common to both *Heterandria* and *Xiphophorus* (from Rosen 1979, Fig. 50, p. 373).

2.3.3.2 Ancestral species maps—Wiley's method (1980, 1981)

In reviewing Rosen's *Xiphophorus* and *Heterandria* data, Wiley (1980, 1981) took the view that all the species events for the Middle American monophyletic groups were the result of successive vicariance events; all dichotomies in the cladograms are the result of formation of natural barriers, followed by speciation. Therefore, Wiley treated the generalized tracks of both groups as equivalent to the distribution of two ancestral taxa. He considered this assumption valid because the overall distribution of both groups extended well beyond the Middle American region. It overcame the problem of unique events within each taxon (see Fig. 2.17). Indeed, the first speciation events were unique for both *Xiphophorus* and *Heterandria*. The initial event was the origin of *Xiphophorus pygmaeus* and *X. nigrensis*, and all other *Xiphophorus*, from the common ancestor, and a unique event which isolated *H. attenuata* in area 6 (Fig. 2.17a, b). The second event was common to both genera and involved the vicariance of area 1 from the rest of the ancestral range. This resulted in the origin of *H. jonesi* and the ancestor of the two remaining area 1 *Xiphophorus* species (*X. montezumae* and *X. cortezi*; see also Fig. 2.11), although Wiley did not include it on his maps. The subsequent division of these two species further subdivided area 1. We conclude that the vicariance event dividing *Xiphophorus* into two areas, 1a and 1b, did not affect *Heterandria*. Wiley believed that two separate and unique events occurred in each genus; *Xiphophorus clemenciae* originated in area 3 and *Heterandria litoperas* originated in area 9 (Fig. 2.17d). The next event was common to both groups and involved a separation of a central western part of the ancestral range (Fig. 2.17e). A subsequent event separated the southern portion of the remaining ancestral range, and the origin of *Xiphophorus* 'PMH' and *Heterandria anzuetoi* (Fig. 2.17f). The next event was the unique origin of *H. cataractae* in area 7 (Figs 2.17g, 2.10), and finally the peripheral isolation and origin



Fig. 2.17 Inferred sequence of speciation and ancestral area maps for *Heterandria* and *Xiphophorus*. In each diagram stippled areas are inferred ancestral ranges. The phylogenetic position of this ancestral species is represented by the unnumbered branch in the area cladograms above and below the biogeographic map. Numbered branches correspond to species represented by the number of the area they inhabit. Common speciation events in the history of the two groups are labelled on the area cladograms as C1-C4. These labels correspond to the original area cladogram of each species group. (Redrawn from Wiley 1981, Fig. 8.16, p. 303.)

of *Xiphophorus signum* and *Heterandria dirempta* which were isolated in area 8 from the remaining taxa, *Xiphophorus helleri* and *Heterandria bimaculata*, in area 2 (Fig. 2.17).

The cladogram in Fig. 2.18 summarizes the sequence of Wiley's successive speciation events from an ancestral species as a single hypothesis for relationships of the areas of endemism. The result provides an hypothesis for his 11 areas and is, in this sense, more complete than Rosen's (1979) analysis. It must be criticized, however, because the method introduces evolutionary assumptions and a degree of interpretation not supported by the data, especially for areas 3, 6 and 9. One 'evolutionary assumption' is that vicariance is the cause of speciation, an assumption made also by Hovenkamp (1997). Wiley's analysis 'works' for *Xiphophorus* and *Heterandria* because the genera have concordant area cladograms, hence shared history, as found by Rosen (1979). If the two genera did not share a history, and, further, if the distribution of one genus was best explained by vicariance and the other by dispersal, Wiley's method would not recognize separate histories, or modes of speciation, for each genus (see also Carpenter 1993).

2.3.3.3 Component analysis: lizards, frogs, and birds

Incongruence can occur between two or more cladograms for a host of reasons. Different groups of organisms exhibit older or younger patterns than the groups to which they are being compared, or they show redundant information due to extinction in one area and unresolved relationships. Variation in the different patterns, effectively the same as sampling errors, lead to errors in predicting patterns of area relationship.

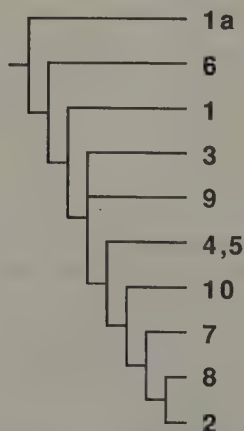


Fig. 2.18 Consensus cladogram for *Heterandria* and *Xiphophorus* based on Wiley's ancestral area maps. See Fig. 2.17 and text for explanation.

The problems of redundant, missing, and ambiguous information can be addressed using component analysis (Nelson and Platnick 1981). To demonstrate component analysis, consider four areas of endemism, A–D, and the hypothetical distributions of three different monophyletic groups of lizards, frogs, and birds, occurring in those areas of endemism (Fig. 2.19). Nelson (1984) introduced this example noting that it was as intuitively opaque to analysis as any he could possibly devise, since it contains almost all of the difficulties encountered in biogeographic analysis.

2.3.3.4 Missing areas

The cladograms in Fig. 2.19a–c all have three areas but area D is ‘missing’ from the lizard cladogram (a), and area A is missing from the frog and bird cladograms (b and c respectively). As Page (1989c) pointed out, the problem of ‘missing’ areas is trivial because if an area is not present it cannot provide any information of area relationships. As shown below, however, the problem is acute when it is necessary to combine two or more cladograms into one general area cladogram that can be reconciled with the lizard, frog, and bird cladograms.

2.3.3.5 Widespread taxa and redundancy

Widespread taxa are uninformative by comparison to area relationships derived from endemic taxa (Platnick and Nelson 1978). Widespread taxa introduce complications into biogeographic analysis because they obscure resolution and introduce redundancy by representing areas more than once on the terminals of any given cladogram. Widespread taxa occur for a variety of historical reasons. Platnick and Nelson (1978) concluded that only phylogenetic hypotheses can dictate area relationships in biogeography. To overcome the problems of widespread taxa and redundancy of distributions, Nelson and Platnick (1981) introduced two critical but rather cryptically named principles—assumptions 1 and 2—which allowed the logical

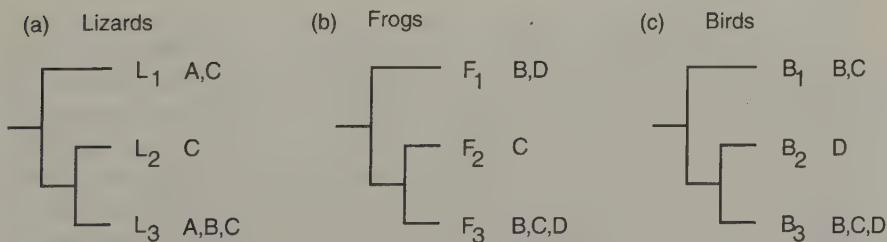


Fig. 2.19 Hypothetical cladograms for (a) lizards, (b) frogs, and (c) birds occurring in four areas A–D.

selection and manipulation of particular areas. Zandee and Roos (1987) later named assumption 0 (see 2.3.3.8 below) under which widespread taxa require a close relationship of the areas in which they occur. Assumptions 1, 2, and 0 treat widespread taxa differently. For a taxon such as the lizard, L_3 in Fig. 2.19a, widespread in areas A, B, and C, assumption 0 treats ABC as a node, with the areas forming a monophyletic group; assumption 1 allows A, B, and C to form either a monophyletic or paraphyletic group; assumption 2 allows all possibilities, that is, A, B, and C may form a monophyletic, paraphyletic, or polyphyletic group. We look at how these different assessments of information provided by widespread taxa affect the results of biogeographic analysis below.

2.3.3.6 Assumption 1

Consider, in Fig 2.19a, the cladogram showing the interrelationships of three lizards, L_1 – L_3 . L_1 occurs in two areas, A and C, L_2 in area C, and L_3 is widespread in areas A–C. Under assumption 1, Nelson and Platnick (1981) argued that whatever was true for L_1 in area A in terms of its relationships with L_2 and L_3 in areas A, B, and C was also true for L_1 in area C. Even if L_1 could be resolved into two taxa, say L_X and L_Y , occurring in areas A and C respectively, the general area relationships could either be monophyletic (Fig. 2.20a) or paraphyletic (Fig. 2.20b,c).

Similar arguments can be applied to L_3 in areas A–C as summarized in Fig 2.20 (and the other cladograms, Fig. 2.19b,c). The three occurrences of L_1 – L_3 in C and the two occurrences of L_1 and L_3 in A could be explained by extinction of L_1 in area B and of L_2 in area A and C, leaving the one occurrence of L_1 in A and C as relicts of an older pattern. Consequently, assumption 1 assumes that only speciation and extinction have occurred (Page 1989c; Fig. 2.20d). Alternatively, it is worth noting that L_1 could have dispersed from area A or C to either C or A, and L_3 could have dispersed from A, B, or C to the other two areas (Fig. 2.20d) to explain the original cladogram in Fig. 2.19a. Therefore, the cladograms are silent about the cause of the pattern.

2.3.3.7 Assumption 2

Consider again the lizards in Fig. 2.19a. Nelson and Platnick (1981) argued that, under assumption 2, whatever was true for L_1 in area A with respect to its relationships with L_2 and L_3 in areas C and A–C respectively, was not necessarily true for L_1 in area C. For example, L_1 could have originated in C and dispersed to A or originated in the ancestral area AC. Also, L_1 could have done this along with L_3 (with respect to areas A, C), and with L_2 (with respect to area C). Consequently, there are now two possibilities for further biogeographic analysis (see the top line in Fig. 2.21). This suggests that for L_1 either area A or C is

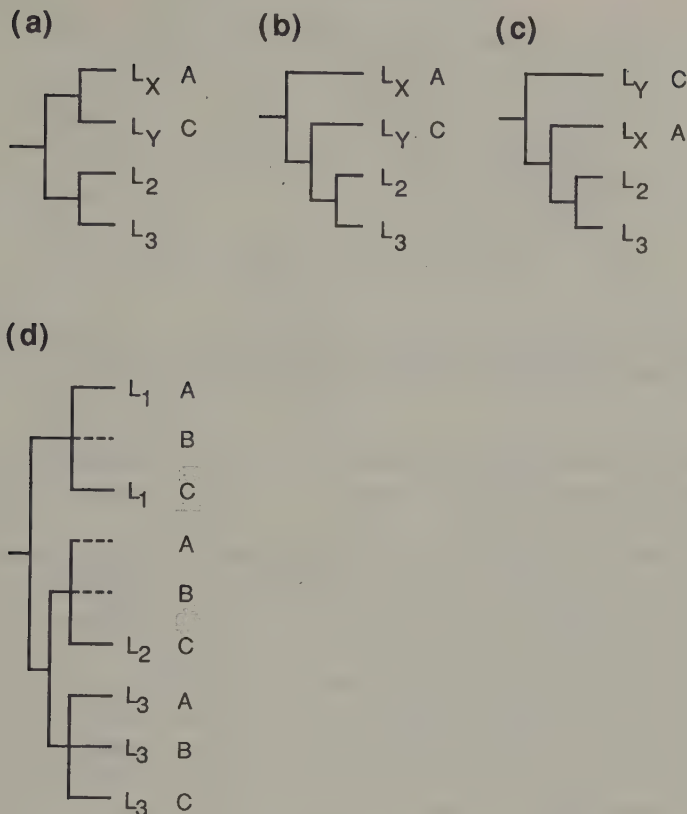


Fig. 2.20 (a–c) Three cladograms derived from the lizard cladogram in Fig. 2.19a under assumption 1. (d) The triple occurrence in area C of L_1 – L_3 and the double occurrence in area A of L_1 and L_3 explained by extinction (single lines) of L_1 in area B and L_2 in areas A and B. Alternatively, by dispersal of L_1 in area A to area C (or vice versa), or by dispersal of L_3 from A, B, or C to the other areas.

redundant. Under assumption 2, unlike assumption 1, speciation, extinction, dispersal, and failures to vicariate are accommodated, but without incorporation of any particular hypothesis *a priori*. The lizard cladogram (Fig. 2.19a) presents six possible area relationships for further analysis, although here there is only one (A(CB)) which is a three-area statement, worthy of further analysis (Fig. 2.21*).

Similar combinations for frogs and birds lead to five cladograms available for component analysis (Fig. 2.22c). Fig. 2.22a shows the five positions available to place the missing area D on to the lizard cladogram. The

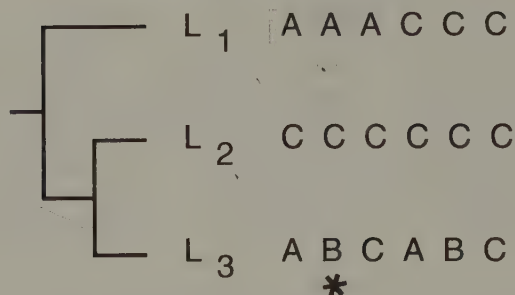


Fig. 2.21 Six possible area cladograms derivable from the lizard cladogram in Fig. 2.20 under assumption 2. There is one three-area statement, $(A(C, B))^*$.

five possible positions are elaborated in Fig. 2.22b. Considering the lizards together with frogs and birds means that there are 25 positions to place the missing areas (Fig. 2.22c).

When we examine all possible cladograms available for each of the original lizard, frog, and bird cladograms, we see patterns unique to the frogs and birds, and patterns in pairs of taxa—three common to lizards and frogs, one pair each for lizards and birds, and four pairs for frogs and birds (Fig. 2.22d). In this example, there is only one pattern common to all three groups which expresses the relationships as $(A(B(C, D)))$ (Fig. 2.22d*). Thus, in the solution to the original problem (Fig. 2.19), we can state that if there is one common history that explains area relationships, that pattern common to all three taxa must be the defensible hypothesis.

Comparison of the results with the original area cladograms (Fig. 2.19a–c) reveals which areas transmit the historical signal and which suggest alternative patterns. For example, in the lizard cladogram, L_1 originated in area A, L_2 in area C, and L_3 in area B. In other words these areas are the signal, and areas C for L_1 , and A and C in L_3 , suggest different scenarios, a form of biogeographic noise or what we may call ‘biogeographic homoplasy’. Likewise, for the frogs, F_1 is considered to have originated in area B, F_2 in area C, and F_3 in area D, and for the birds, B_1 originated in area B, B_2 in area D, and B_3 in area C.

2.3.3.8 Assumption 0 and Brooks parsimony analysis

In developing a method for studying host/parasite relations, Brooks (1981, 1985, 1990; see also Wiley 1987; Brooks and McLennan 1991) derived an additive binary coding procedure which assumed that when several hosts were infected with one species of parasite, that group of hosts is monophyletic. Similarly, when one host was infected with more than one species

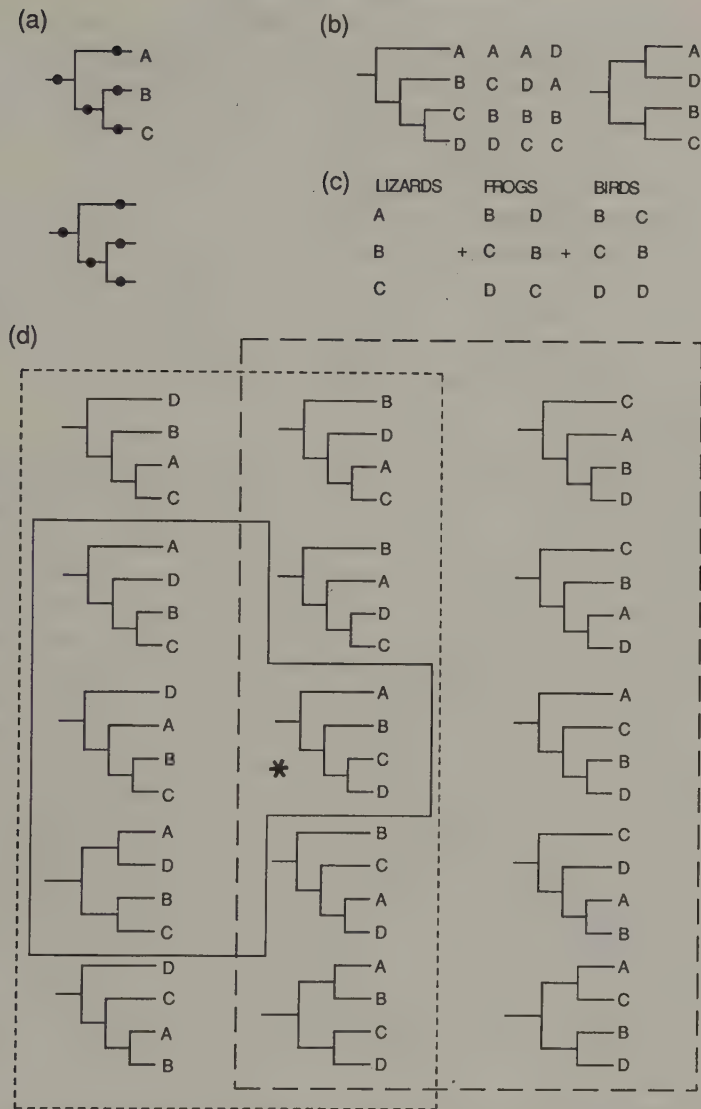


Fig. 2.22 (a) Cladogram for three species of lizards in areas A-C. The filled circles show possible points of addition for the 'missing' area D. (b) The five cladograms obtained by addition of area D to the five possible positions. (c) The five informative cladograms for lizards, frogs, and birds, available for further analysis after application of assumption 2 to the cladograms in Fig. 2.19. (d) Intersecting cladograms obtained by addition of 'missing' area D to the lizards cladogram and area A to the frogs and birds cladograms in c. The cladograms of lizards (full lines), frogs (long dashes), and birds (short dashes) display unique patterns and a variety of partial intersections, but only one cladogram $*(A(B(C, D)))$ is common to lizards, frogs, and birds.

of parasite belonging to the same group then that condition should be assumed to specify monophyly. The method has been described as 'Brooks parsimony analysis' (BPA) by Wiley (1987). An analogy between patterns of host/parasite and taxon/area relationships has been explored using BPA by a variety of authors (e.g. Wiley 1987, 1988, 1989; Mayden 1989; Brooks and McLennan 1991; Wiley *et al.* 1991).

Zandee and Roos (1987) argued that areas occupied by a widespread taxon are unquestionably monophyletic. In the spirit of Nelson and Platnick (1981), they termed this principle assumption 0. Both assumption 0 and BPA treat areas occupied by widespread taxa as monophyletic (see also Mickevich 1981). They differ in treatment of missing areas (Page 1990a): in BPA, missing areas are uninformative; under assumption 0, they are primitively absent.

The lizard, frog, and bird data were coded for BPA (Fig. 2.23a–c, Table 2.1). Each node is numbered. An area by node matrix is coded; presence of the area included in the node is coded as 1, absence as 0 (Table 2.1). If two or more groups of taxa are being analysed together, and an area is not occupied by members of some group(s), that area is coded as missing (?) in the matrix for that group(s). The matrix for the lizard, frog, and bird distributions (Fig. 2.23) was analysed using the Wagner parsimony criterion as implemented in *Hennig86* (Farris 1988; an alternative parsimony program, *PAUP* (phylogenetic analysis using parsimony), is given by Swofford 1991a). When using an all-zero outgroup, two cladograms were obtained (Fig. 2.23d,e), neither of which recovers the intersecting set (A(B(C, D))) (Fig. 2.22d*). Because coding under BPA with assumption 0 provides resolutions of area relationships other than those supported by the original distribution patterns, the results obscure rather than clarify area relationships. For further comparisons of BPA with other cladistic biogeographic methods, see Platnick (1988), Humphries (1989), Page (1990b), Nelson and Ladiges (1991b), Ronquist (1997), van Soest and Hajdu (1997), and De Jong (1998).

Table 2.1 Codes for Brooks's Parsimony Analysis scored from the cladograms in Fig. 2.23. See text for explanation.

Taxa	Characters														
	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1
										0	1	2	3	4	5
A	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
B	1	0	1	0	1	1	1	1	0	1	1	1	1	0	1
C	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1
D	0	0	0	0	0	1	1	1	0	1	1	0	1	1	1

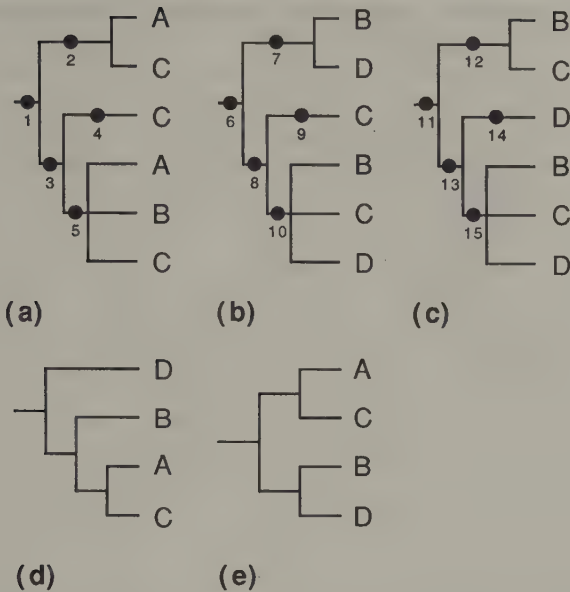


Fig. 2.23 (a–c) Lizards, frogs, and birds; the cladograms coded using BPA coding method. (d,e) Two trees obtained using a parsimony algorithm on the area by node matrix. See text for explanation.

2.3.3.9 Platnick's (1981) analysis of Rosen's poeciliid data; Page's *COMPONENT* program (Page 1989a–c, 1993a)

Each of the two widely distributed poeciliid fish genera, *Heterandria* and *Xiphophorus*, has species in 11 identifiable, disjunct areas. The area cladograms are shown in Fig. 2.24 calculated for assumptions 0, 1, and 2 with *COMPONENT* 1.5 (Page 1989a–c). Areas originally numbered 4 and 5 are occupied by one species in each genus and thus may be analysed as a single area. Area 11 was treated by Rosen (1978, 1979) as a putative hybrid area between areas 4/5 and 2. Following Platnick (1981) and Page (1989a–c) it is omitted from the analysis.

A comparison of the two taxa (Fig. 2.24) shows that *Xiphophorus* is less informative than *Heterandria* because it has two widespread species in areas 4/5, 6, 9, and 10, and is not present in area 7. For *Heterandria*, areas 4/5, 6, 9, and 10 are all occupied by endemic species. Again, under assumption 1 whatever is true of a widespread taxon in one part of its range (e.g. *Xiphophorus alvarezii* in area 4/5) must be true in the other part of its range (i.e. area 6). Under assumption 2, however, what is true of a widespread taxon in one part of its range need not also be true of the taxon elsewhere. In other words, widespread distributions tell us that we are ignorant of the

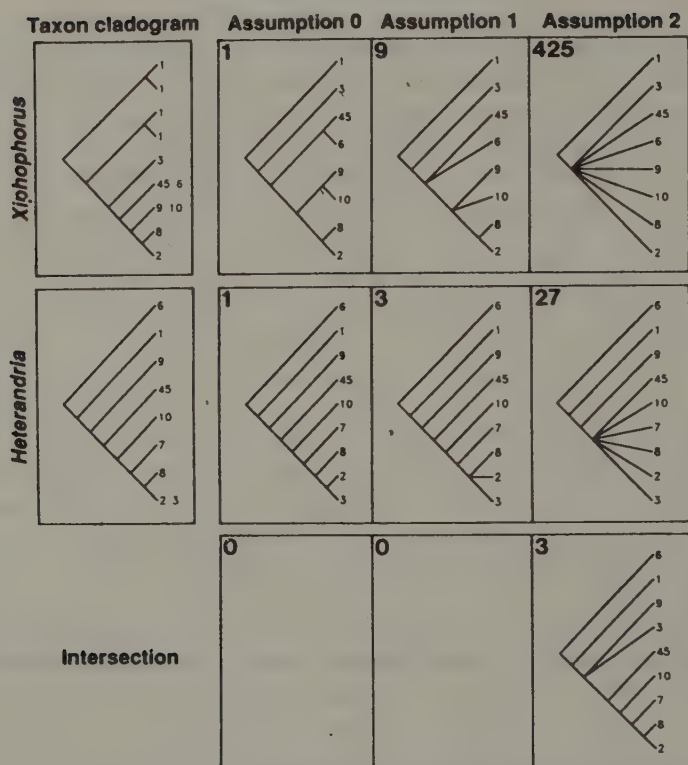


Fig. 2.24 Re-analysis of Rosen's (1978, 1979) data. For *Xiphophorus* and *Heterandria* the taxon cladogram and Nelson and majority rule consensus trees analysed under assumptions 0, 1 and 2 are shown. The number in the top left corner of each box displays the number of equally parsimonious area cladograms obtained with *COMPONENT* 1.5. The intersection is the set of three area cladograms common to *Xiphophorus* and *Heterandria*. (Redrawn from Page 1989c p. 265.)

reasons for lack of resolution in the cladogram; we do not know whether the patterns are due to dispersal or a failure to speciate in response to a vicariance event. Rosen's original (1978, 1979) application of the Platnick and Nelson (1978) biogeographic method compared the two cladograms (Fig. 2.15a,b) to one another and identified only those parts that were congruent, which meant that a cladogram for only six areas could be produced (Fig. 2.16).

Platnick (1981) equated removal of unique and incongruent areas with analysing under assumption 1. Page (1993a) used the same procedure to find the common pruned tree. If assumption 1 is adopted, then the

Xiphophorus populations of area 9 must be most closely related to the population in area 10, and the information on area 9 is incongruent with the information from *Heterandria*. The information on area 6 is also incongruent on both cladograms. Hence, the nine trees for *Xiphophorus* and the three trees for *Heterandria* do not intersect. A different result is obtained by applying assumption 2. By taking the information on areas 6 and 9 from *Heterandria* as correct, the incongruent information in the same areas for *Xiphophorus* is due either to dispersal or a failure to speciate in response to a vicariance event. Rosen applied a tree-pruning procedure because when groups dispersed or failed to respond to vicariance events, information was reduced. Platnick (1981) noted, however, that if widespread taxa are uninformative they cannot be incongruent at the same time.

Taken on their own, cladograms with widespread taxa analysed under assumption 2 give uninformative components, but when considered with other cladograms involving widespread taxa informative results are possible. Under assumption 2 the *Xiphophorus* cladogram (Fig. 2.24) allows the populations in area 9 or 10 (but not both) and area 4/5 or 6 (but not both) to occur in any of 12 positions, on nearly all the branches of the cladogram. Of the 425 possible trees for *Xiphophorus*, and the 27 for *Heterandria*, there are three intersections. These can be summarized, using either Nelson or majority rule consensus trees, as a trichotomy, as shown in Fig. 2.24. For a review of the definitions of consensus trees, see Swofford (1991b).

2.3.3.10 Comparing cladograms and applying parsimony (Page 1989b)

As also noted in Section 2.3.3.8 above, coding methods for converting trees into data matrices were described by Wiley (1987), Zandee and Roos (1987), Humphries *et al.* (1988), Kluge (1989), Brooks and McLennan (1991) and Wiley *et al.* (1991) (see also Fig. 2.23, Table 2.1) to implement the parsimony criterion in cladistic biogeography. Although Zandee and Roos (1987) devised a method to code for assumptions 0, 1, and 2, Page (1989b) pointed out that the implementation of assumptions 1 and 2 into their parsimony/clique method for combining trees is incomplete because it does not adequately interpret redundant distributions.

The Wagner tree approaches of Wiley (1987), Kluge (1989), and Humphries *et al.* (1988), and the parsimony/clique method of Zandee and Roos (1987; see also Zandee 1987, 1991), require complex interpretations of area homoplasy to account for results. Application of parsimony to biogeography, while accepting completely the analogy between characters/taxa and taxa/areas, is likewise inappropriate. For example, equally parsimonious reconstructions with different patterns of area homoplasy means

that different historical scenarios can be postulated for the same cladogram (Brooks 1985; Page 1989b).

How can parsimony be applied to the comparison of cladograms? There are two methods embodied in Nelson and Platnick (1981), which have become later described as 'three-item statements analysis' and 'fit or reconciliation analysis'. Page (1989b) showed that fit or reconciliation analysis related to the 'fit' algorithm of Goodman *et al.* (1979) for reconciling gene trees and organism phylogenies. Page's fit analysis is highly appropriate for comparing trees in biogeography and host/parasite relations (Page 1989b). The implications of both of these methods for Rosen's fish data are outlined in the following two sections.

2.3.3.11 Reconciling trees and the 'fit' analysis of Page (1993a,b)

The measure of degree of fit between two trees was defined by Nelson and Platnick (1981, p. 417) as the difference in the number of nodes in the original cladogram and the reconciled tree; the extra nodes and branches required to make the fit they termed 'items of error'. Goodman *et al.* (1979) and Nelson and Platnick (1981) independently developed the same method for mapping one tree on to another to reconcile them as shown by Page (1993a,b). To explain incongruence between two trees, both papers describe a method for invoking the presence of unrecognized multiple lineages in one of the trees to make it fit with the other(s) (Page 1993b). Nelson and Platnick (1981, pp. 410–67) described the effects of poor taxonomic sampling and extinction, among other factors, that could lead to incongruence between area cladograms for different taxa. They suggested that in the presence of two or more sympatric lineages, poor sampling could obscure the underlying area relationships for the same reason that sampling from a collection of paralogous genes may give a confused picture of species relationships (see Page 1993b, 1994). Mapping different lineages on to one another was also invoked by Humphries *et al.* (1986) and Linder and Crisp (1996) in their studies of cospeciation between *Nothofagus* and its parasites.

Tree mapping is designed to analyse historical associations between any 'host' and 'associate' relations (Page 1993a,b; Table 2.2). Reconciling an associate cladogram with a cladogram for the hosts (and this could mean parasites on hosts, taxa within areas, and gene trees onto species trees—see Table 2.2), assumes that the host–associate relationship is due to association by descent (Mitter and Brooks 1983; Brooks and McLennan 1991). This provides a measure of fit between host and associate trees which can be tested statistically and can also generate hypotheses about relative ages of divergence events in the two lineages (Page 1993a,b).

Given incongruence between general area cladograms (hosts) and the original area cladograms such as those for *Heterandria* and *Xiphophorus* (associates), it is possible to reconcile the two original cladograms with the

general area cladogram so that the observed associate relationships and host associations can be explained solely by association by descent. In *COMPONENT* 2.0 for Windows®, Page (1993a) developed an algorithm in which the observed associate cladogram was a subtree of a larger tree. By default, *COMPONENT* 2.0 maps all associates directly onto host tree(s). This is equivalent to assumption 0 (Zandee and Roos 1987; Page 1990b). Because two or more areas may share the same widespread taxon due to geographical proximity rather than close relationship, widespread taxa can be misleading.

COMPONENT 2.0 offers the option of mapping widespread taxa under assumption 1 (Nelson and Platnick 1981; Page 1990b) because the algorithm attempts mapping associate trees on to the general area cladogram by fitting at nodes (i.e. shared ancestral nodes). Assumption 2 is not implemented directly in *COMPONENT* 2.0, yet it can be by deleting all but one area from the range of each widespread taxon before generating the area cladogram. For *Xiphophorus* and *Heterandria* this amounts to one analysis for assumption 0 and eight separate analyses for assumption 2 (Table 2.3). Under the default analysis (effectively assumption 0) the original area cladograms for *Heterandria* and *Xiphophorus* (Fig. 2.13) can be mapped on to the general area cladogram (Fig. 2.25a) to produce two reconciled trees (see Fig. 2.25b,c). Note that the reconciled tree for

Table 2.2 Kinds of historical associations

Hosts	Associates
Organisms	Genes
Host organisms	Parasitic organisms
Areas	Organisms

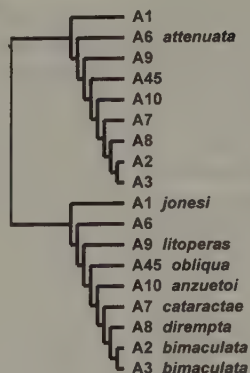
Table 2.3 Items of error for reconciling *Heterandria* (H) and *Xiphophorus* (X) to area cladograms analysed under the default assumption and assumption 2

	Default		Assumption 2	
	H	X	H	X
Duplications	2	1	0	0
Total leaves	26	15	8	6
Leaves	18	9	0	0
Losses	8	5	0	0

(a)



(b)



(c)



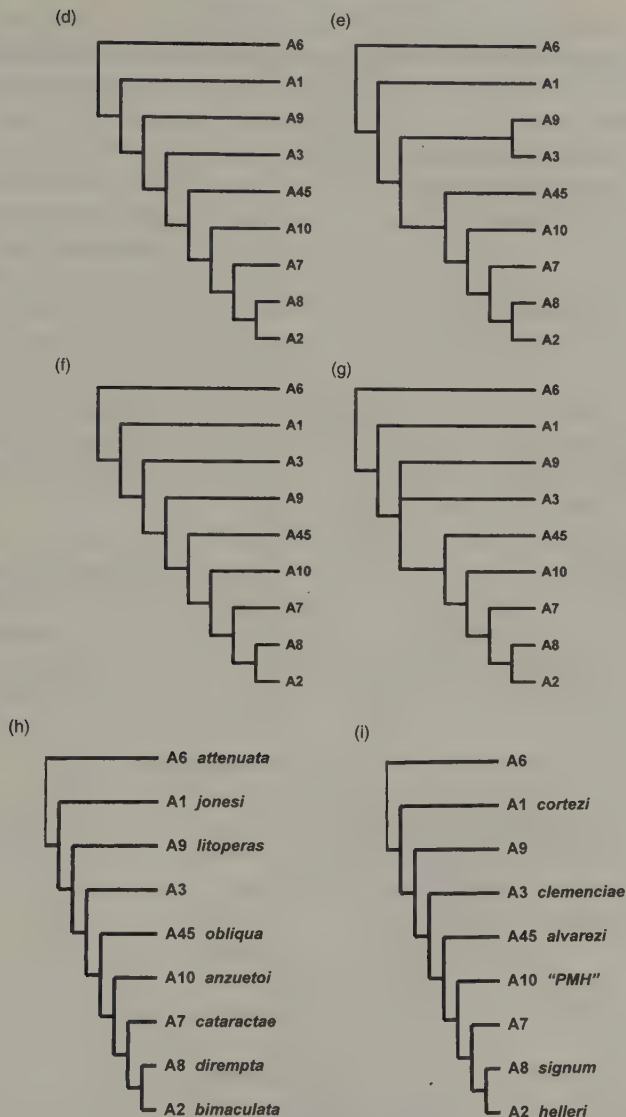


Fig. 2.25 Reconciliation of trees using *COMPONENT* 2.0. (a–c) Reconciliation of trees using the default options. (d–i) Reconciliation of trees using assumption 2. (a) Host area cladogram produced using heuristic search options. (b) Cladogram of *Heterandria*. (c) Cladogram of *Xiphophorus*. N.B. *Xiphophorus* is absent from area 7. (d–f) Three trees for the *Heterandria* and *Xiphophorus* cladograms using assumption 2. (g) Strict consensus tree for the three trees obtained by heuristic search using assumption 2. The trees differ only in the relative positions of areas 3 and 9, that is whether they are sister to each other or either is sister to the area clade 45–2. (h, i) The reconciled trees for *Heterandria* and *Xiphophorus* cladograms mapped on to one of the area cladograms in (f). All three area cladograms gave equally parsimonious fits for the species cladograms.

Heterandria (Fig. 2.25b) consists of the host (area) cladogram duplicated. The node at which the two subtrees are rooted corresponds to an event that gave rise to two lineages. *COMPONENT* 2.0 distinguishes between two kinds of duplication; that required because the general area cladogram and original area cladograms are incongruent (as in the above example) and that required because the descendants of a given associate have overlapping host ranges. Under the default option, reconciliation for *Heterandria* gives one duplication, 10 added branches, and three lost branches. For *Xiphophorus*, three duplications are needed, 22 added branches, and 15 lost. The results are a poor fit compared with those obtained under assumption 2. Although there are three possible host cladograms (Fig. 2.25d–f; the strict consensus tree is given in Fig. 2.25g) the fits for *Heterandria* and *Xiphophorus* are remarkably good (Fig. 2.25h and i) and equally parsimonious for the three trees; that is, a total of eight and six branches corresponding to the terminal branches of the primary cladograms (Fig. 2.25d–f), and no duplications added or losses postulated (Table 2.3).

The trees generated with assumptions 0 and 1 show less than optimal reconciliation with the original area cladograms (see Table 2.2, based on the trees given in Fig. 2.25). Assumption 2 is the optimal procedure for determining ‘fit’ between original area cladograms with widespread taxa, possible extinctions, or poor samples of taxa; the best fit is given in Fig. 2.26. Under vicariance, this means that *Xiphophorus* failed to respond to

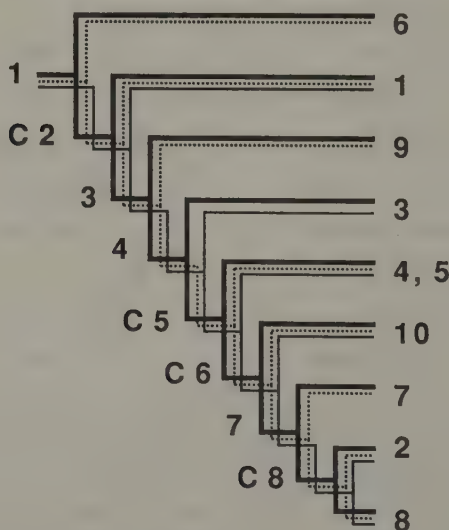


Fig. 2.26 Scenario combining the area cladogram (thick solid lines) and the best fitting cladograms of *Heterandria* (dotted line) and *Xiphophorus* (thin solid line) determined under assumption 2 (see text for explanation).

the isolation event at node 1, separation of area 6. Both genera responded to the second event at node 2, the separation of area 1 and the rest, but again *Xiphophorus* failed to respond to the event at node 3. Both taxa responded to vicariance events at nodes 5 and 6. Presence of *X. alvarezi* in area 6 and *X. 'PMH'* in area 9 may be interpreted as dispersal events. *Xiphophorus* failed to respond to the vicariance event at node 7, both responded to the event at node 8, and presumably the presence of *H. bimaculata* in area 3 is due to dispersal.

2.3.3.12 Three-item statements (Nelson and Ladiges 1991a-d; Nelson and Platnick 1991)

Since the first description of three-item statements, buried in the heart of their 1981 book, Nelson and Platnick (1991) have developed a method to implement parsimony into systematics and biogeography, which they call *Three-Item Statements Analysis*. Nelson and Ladiges (1991a,d) have written a series of interactive computer programs that code character data for taxonomic analysis of three-taxon statements (*TAX*) with Wagner parsimony programs such as *Hennig86* and *PAUP*, and distributional data for taxon cladograms as suites of three-area statements (*TAS*) to generate trees that are supposedly based on a higher information content than hitherto recognized. As distinct from Wagner parsimony methods, Nelson and Platnick (1991) claim that the three-item approach has the advantage of teasing out not only *component* information but also *term* information (*sensu* Mickevich and Platnick 1989). The method has been applied in a re-analysis of Mayden's (1989) data on North American freshwater fishes (Nelson and Ladiges 1991c), eucalypts (Ladiges *et al.* 1992), and a variety of taxa (Morrone and Carpenter 1995, for example). Here, we apply the method in a theoretical example to show how the method codes data, and then to the *Xiphophorus* and *Heterandria* data using assumptions 0, 1, and 2.

To describe coding for assumption 1, Fig. 2.27 is a cladogram for four taxa that live in four areas: two taxa are endemic, one to area A and one to area C; two are widespread in areas BC and AD. For node 1, there are two branches, BC and ADC, with A as the root. The three-area statements for node 1 are (A(BA)), (A(BC))* , (A(BD))* , (A(CA))* , and (A(CC)), three of which are informative (*). For node 2, there are two branches, AD and C, with A, B, or C as possible roots. The six three-area statements for node 2 are (A(AC)), (A(DC))* , (B(AC))* , (B(DC))* , (C(AC)), and (C(DC)), three of which are informative (*).

Only the six informative statements become characters for a matrix (Table 2.4). Of the six characters, 2 and 3 are the same; they could be coded as one character with a weight of 2. *TAS* identifies repeated characters and calculates weights to minimize the matrix. Parsimony analysis

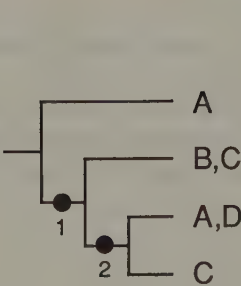


Fig. 2.27 Coding nodes for the application of assumption 1 in three-area statements analysis.

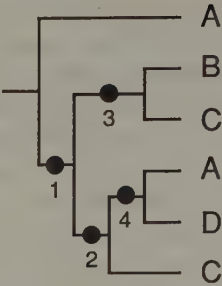


Fig. 2.28 Coding widespread taxa as nodes, for applying assumption 0 in three-area statements analysis.

Table 2.4 Data matrix generated from the informative three-area statements in Fig. 2.27

Area	0	1	2	3	4	5
Outgroup	0	0	0	0	0	0
A	0	0	0	0	1	?
B	1	1	?	?	0	0
C	1	?	1	1	1	1
D	?	1	1	1	?	1

under assumption 1, using an all-zero outgroup, gives the area cladogram (A(B(CD))).

To code for assumption 0, widespread taxa are treated as nodes, here numbered 3 and 4 in Fig. 2.28. Node 3 specifies three informative three-area statements: (A(BC))*, (A(BC))*, and (D(BC))*, the first two of which are identical; an additional statement, (C(BC)), is uninformative. Node 4 specifies (A(AD)), (B(AD))*, (C(AD))*, (C(AD))*, the last three of which are informative (*), the last two of which are identical. Parsimony analysis of these six informative characters, together with those for nodes 1 and 2, implements assumption 0. With uniform weight, three trees of length 17, consistency index (CI) 0.70, retention index (RI) 0.58 (see Farris 1989) are calculated: (A(B(CD))); (A(D(BC))); ((B,C)(AD)). The strict consensus of these three trees is shown in Fig. 2.29 (coding following Nelson and Ladiges 1991d).

Currently, options available to implement assumption 2 in *TAS* are limited. In the example above, however, resolution under assumption 2 by hand gives the same result as assumption 1. The positions of A and C are determined by the endemic taxa, and are ‘removed’ from the other

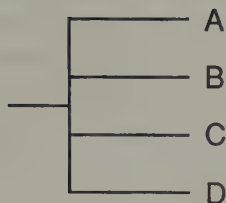


Fig. 2.29 Tree obtained from three-areas statements analysis of the matrix derived from the cladogram in Fig. 2.28.

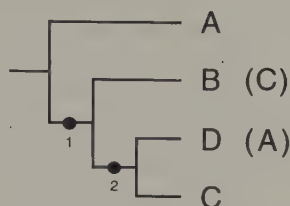


Fig. 2.30 Coding cladograms for three-area statements analysis using assumption 2.

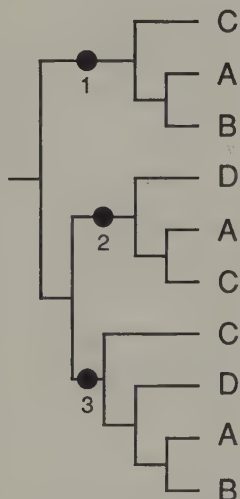


Fig. 2.31 Recommended identification of clades 1-3 for repeated areas using three-area statements analysis.

terminal taxa (Nelson and Ladiges 1991d). One way to approximate assumption 2 using *TAS* is first to reduce the areas for widespread taxa in favour of endemics, and code the cladogram as for assumption 1 (Fig. 2.30). If a cladogram has areas repeated, Nelson and Ladiges (1991b) recommend treating clades (Fig. 2.31) 1, 2, and 3 separately. Combining repeated patterns of areas in biogeography is analogous to confounding gene paralogy and orthology in molecular systematics (Page 1993b).

One distinction between three-area statements and component analysis may be demonstrated by comparing results for the *Heterandria* and *Xiphophorus* data under each protocol. *TAS* obtained resolution of area

relationships under assumptions 0 and 1 (Fig. 2.32a,b) which were not identified as intersecting solutions for these two genera under *COMPONENT* 1.5 (Fig. 2.24). Three-item statements analysis under assumptions 0 and 1 was influenced overwhelmingly by components in the *Heterandria* area cladogram; that is, the *TAS* solutions (Fig. 2.32a,b) and *Heterandria* area cladogram (Fig. 2.24) agree in the apomorphic placement of area 3. Both *TAS* (Fig. 2.32c) and *COMPONENT* 1.5 (Fig. 2.24) retrieved identical solutions under assumption 2.

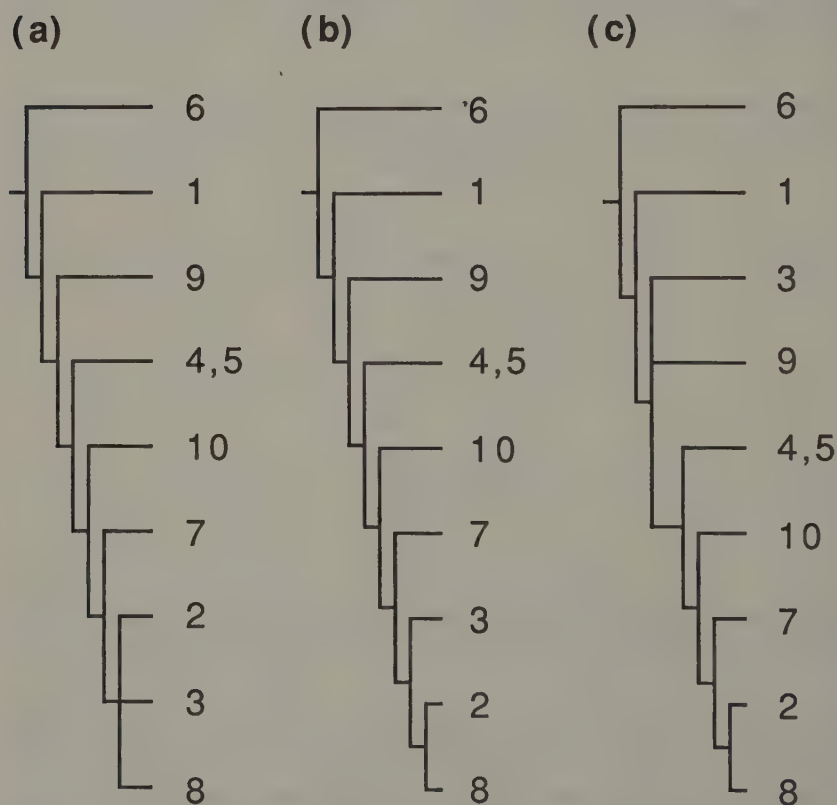


Fig. 2.32 General area cladograms determined for *Heterandria* and *Xiphophorus* using three-area statements analysis. (a) Strict consensus tree of two trees determined under assumption 0—interchangeable for areas 3 and 8 as sister to area 2. (b) One tree obtained under assumption 1. (c) Strict consensus tree for the three trees obtained under assumption 2.

2.3.3.13 Subtree analysis, paralogy, and redundancy in area cladograms (the TASS program of Nelson and Ladiges v. 1.4, 1.5 1994, v. 2.0 1995)

Geographic paralogy is evidenced by duplication and overlap of distributions of organisms at different nodes of area cladograms (Nelson and Ladiges 1991c; Page 1993b). Nelson and Ladiges consider that the problem has come to light because of efforts to apply parsimony methods to biogeography by coding area cladograms into binary matrices of 0 and 1 scores (see, for example, Humphries and Parenti 1986; Wiley 1987; Humphries *et al.* 1988; Kluge 1989; Legendre 1990; Humphries 1992). The implication of geographic paralogy, duplication, and redundancy on area cladograms for biogeography is that nodes retrieved through cladistic analysis of organisms are not directly informative of geographic relationships. Nelson's original investigations using assumption 2 demonstrated that trees with three taxa, e.g. (1(2,3)) with distributions such as, for example, (AC(C,ABC)), really have only one informative statement of area relationships (A(C,B)).

Solutions to the problem of redundancy and paralogy have recently been investigated by Nelson and Ladiges (1996) through comparison of component analysis and three-item statements analysis. The algorithm, *TASS* (Nelson and Ladiges 1994, 1995), can extract unambiguous informative or paralogy-free subtrees from seemingly complex area cladograms and summarize them into binary-coded component matrices or three-item statement matrices. A comparison of the two coding procedures by means of six simple examples allows evaluation of the causes of ambiguity created by paralogy and redundancy in area cladograms (see Fig. 2.33).

Three-item statements are coded from cladograms as described in Section 2.3.3.12. Example 1, Fig. 2.33a, has three areas, which code for two components and one three-item statement. The ABC component (0) of area relationships is uninformative. Example 2 (Fig. 2.33b) shows two sister species, 1 and 2, which both live in area C. Duplication of area C is redundant, reflected by two uninformative components, ABC_1 (0) and ABC_2 (2). There are, however, two three-item statements, $A(BC_1)$ and $A(BC_2)$. Example 3 (Fig. 2.33c) shows redundancy at the basal nodes of the cladogram, as shown by the presence of two species, 1 and 2, in area A. All three nodes are coded in the component matrix, only one of which, BC (node 2), is informative. As in the previous example, there are two informative three-item statements, $A_1(BC)$ and $A_2(BC)$. The fourth example (Fig. 2.33d) is one of redundancy where two taxa, 1 and 2, occur in area C at the basal and terminal nodes of the cladogram. Nodes 0 and 1 both code as uninformative components, ABC, and node 2 codes as the only informative component, BC_1 . By contrast, there are two informative, but

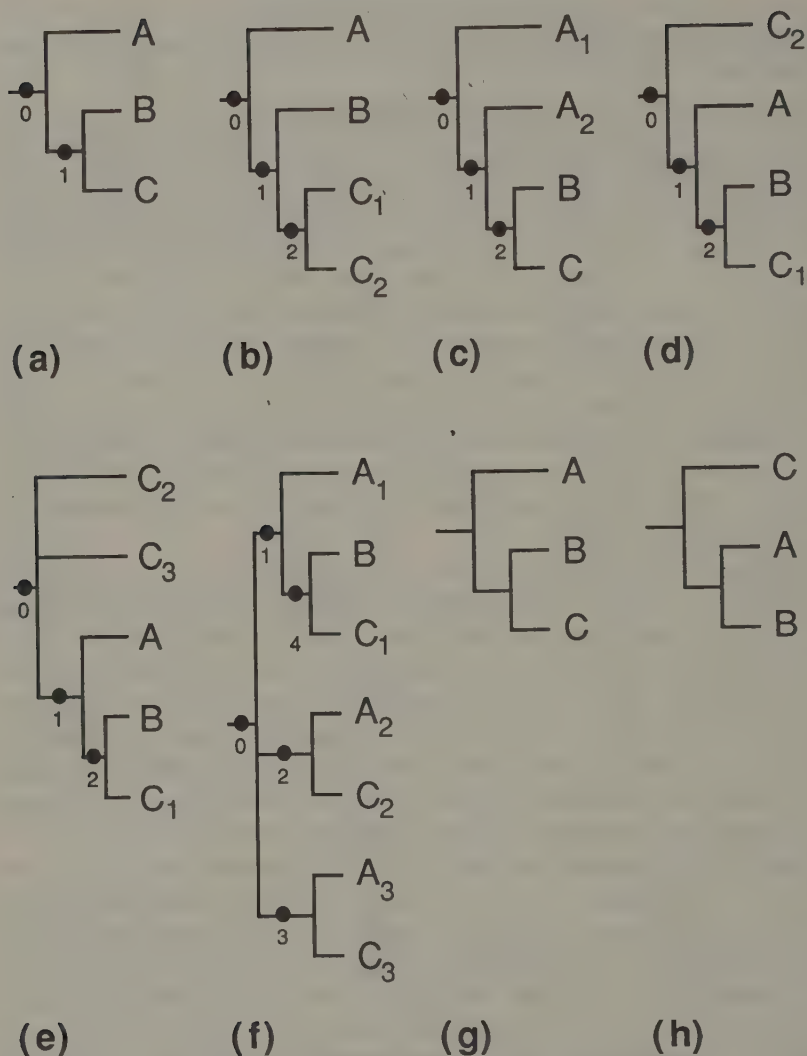


Fig. 2.33 Six examples of coding trees (a–f) for components and three-item statements matrices (after Nelson and Ladiges 1996). (g, h) Informative three-item statements. See text for explanation.

conflicting, three-item statements, $C_2(AB)$ and $A(BC_1)$. Three taxa occur in area C in example 5 (Fig. 2.33e), a cladogram showing redundancy for area C. Here there is only one informative component, BC, (node 2), but three informative three-item statements, $A(BC_1)$, $C_2(AB)$ and $C_3(AB)$. The final example 6 (Fig. 2.33f) shows redundancy for areas A and C with one

duplication for clade AC. Coding of this cladogram gives four informative components (nodes 1–4) and seven informative three-item statements $[(A_1(BC_1); B(A_2C_2); B(A_3C_3); A_2(BC_1); C_2(A_1B); A_3(BC_1); \text{ and } C_3(A_1B))]$.

Nelson and Ladiges argue that these three-item statements represent more completely the geographic information in the original trees of Fig. 2.33a–f. Parsimony analysis yields A(BC) for examples 1–3 (Fig. 2.33a–c), but varying degrees of conflict and ambiguity in examples 4–6 (Fig. 2.33d–f). Our understanding of the six examples is that three-item statements analysis makes a distinction between binary and three-item coding in that they all have the same binary coding (Fig. 2.33g) but different three-item matrices (Fig. 2.33g,h). Although not an exhaustive analysis, the crucial conclusion from these results is that paralogy in area cladograms may be the major cause of conflict in assessment of area relationships. Effects of paralogy are exaggerated at node 2 of example 2 (Fig. 2.33b), node 0 of example 3 (Fig. 2.33c), and node 0 of example 5 (Fig. 2.33e). By removal of redundant terminals, the solution A(BC) is always recovered (Fig. 2.33g).

The effect of subtree and parsimony analyses can be demonstrated with a real example (see Ladiges *et al.*, 1997). The phylogenetic tree for *Nothofagus*, of Linder and Crisp (1996), based on a combined analysis of morphological and molecular data, has 30 terminal taxa occurring in five southern hemisphere areas, Australia, New Zealand, South America, New Guinea, and New Caledonia (Fig. 2.34). Subtree analysis produced three subtrees, each with only one informative node: two independent, but identical groups showing a (South America (Australia, New Zealand)) pattern and one showing the (South America (New Caledonia, New Guinea)) pattern. Analysing both the component matrix and the three-item statement analysis produced one informative solution (Fig. 2.35).

2.4 DISCUSSION

Through exhaustive track analyses Croizat (1952, 1958, 1964) demonstrated that there is tremendous repetition in distribution patterns between widely disjunct areas of endemism. Three decades of research have seen the gradual application of parsimony methods and tree manipulations to render coherent explanations to a mixture of congruent and conflicting geographic patterns. Detecting common components between different cladograms initiated a new research programme designed to recognize historical signals in a sea of geographic homoplasy. Incomplete fits between area cladograms for different groups of organisms due to problems of widespread taxa, unique clades, and ‘missing’ areas were overcome by Nelson and Platnick (1981) through the use of two quite different protocols,

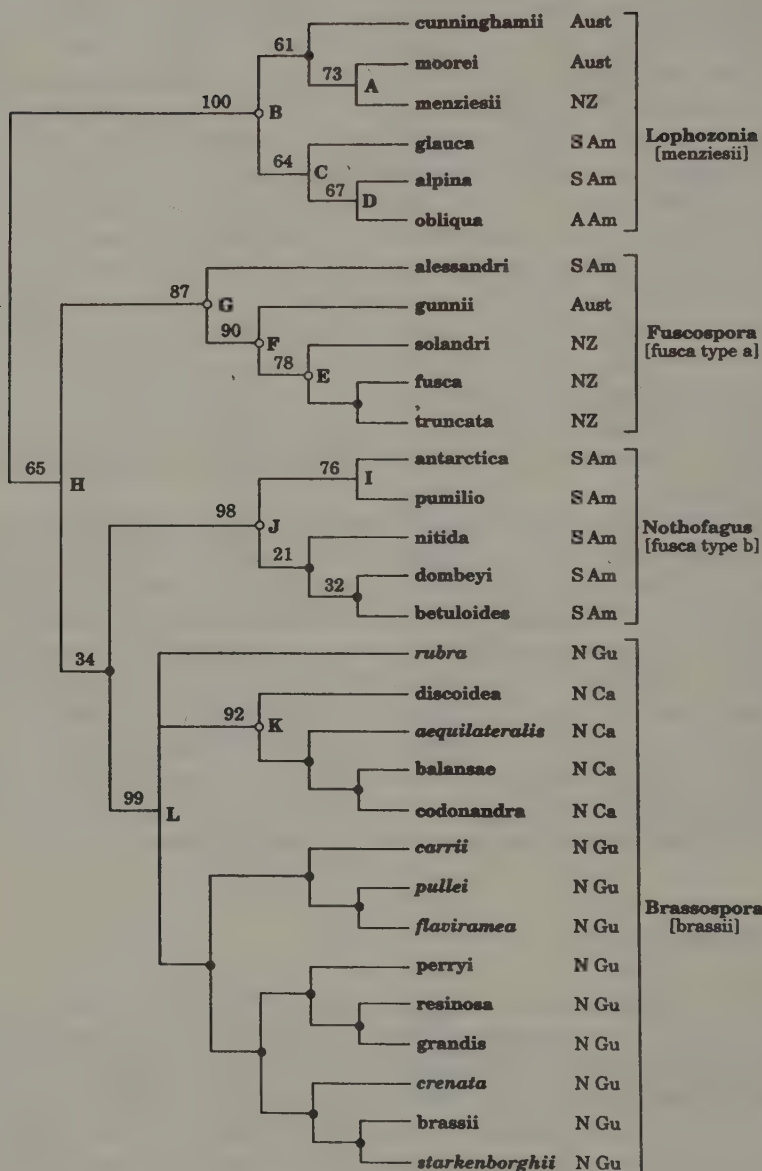


Fig. 2.34 Hypothesized phylogenetic tree for *Nothofagus*, using morphological and molecular (ribulose biphosphate carboxylase, large subunit (rbcL) sequence) data (from Linder and Crisp 1996).

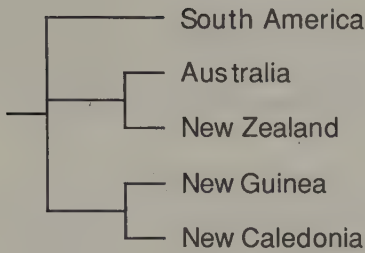


Fig. 2.35 Area cladogram for *Nothofagus* calculated using *TASS*, component coding, and *Hennig86* of the topology in Fig. 2.34. See text for explanation.

assumptions 1 and 2 and ‘tree mapping’, to determine the number of items of error to reconcile one pattern with another, both of which have been taken up by succeeding biogeographers. Computer implementations by Page (1989a, 1993a) have provided a much clearer understanding of the application of both protocols, but frustrations caused by conflicting area patterns remains amongst empiricists (e.g. Crisp *et al.* 1995; Morrone and Carpenter 1995). Nelson and Ladiges (1996) take a similar view:

Subsequent developments within cladistics offered the hope that geographic data, when associated with nodes of cladograms generally and when analyzed by the exact methods of parsimony analysis, would prove coherent—even convincing to other, ecologically orientated, biogeographers and to biologists in general. This hope, still persistent today, seems to have been realized only to a limited degree. It is doubtful, for example, that the accumulated findings of cladistic biogeography of the last two decades have proven more convincing than those of Croizat of the previous few decades . . .

(Nelson and Ladiges 1996, pp. 53–4).

We believe this to be overly pessimistic. Theoretical discoveries always move in fits and starts, and it is clear that the meaning of information in biogeography is still under investigation. The recognition of ‘paralogy’ in area cladograms, and the subtree analyses using *TASS* by Nelson and Ladiges (1996), offer prospects for escaping the myriad trees obtained by other methods. Removing paralogy should lead to straightforward ways of expressing area interrelationships.

2.5 CONCLUSIONS

We hope that, by outlining the methods of cladistic biogeography and re-examining in detail Rosen’s pioneering work on poeciliid fishes, we have underlined the significance of cladistics for historical biogeography.

Comparing Rosen's results with Good's (1974) traditional approach and Croizat's (1958) panbiogeographic method emphasizes that point further. On the basis of plant distributions Good indicated that 'Isthmian America has a close relationship with western North America' (Good 1974, p. 156). He also said:

There is a well-defined line of demarcation (usually described as running from the Gulf of Fonseca on the Pacific coast south-east across Nicaragua to the Caribbean) which may be regarded as the southern limit of the isthmian extension southward of the Rocky mountain system. This area is geologically much younger and has undergone various degrees of subsidence and emergence since the Cretaceous until, in the Oligocene, a great upheaval resulted in the formation of the lands which, to quote a vivid phrase finally sealed the marine portal between North and South America.

Good 1974, p. 233

Only one two-area biogeographic statement is expressed by Good: isthmian America is most closely related to western North America. Croizat's (1958) work is far more detailed. He devotes Chapter VII of *Panbiogeography* Vol. 1 to Central American and Caribbean biogeography, using a variety of botanical and zoological examples. His main conclusions for the Caribbean are best summarized by Rosen (1976) as we noted on p. 54 (see Fig. 2.7). Track analysis yields five main components: a North American-Caribbean track, a South American-Caribbean track, an eastern Pacific-Caribbean track, an eastern Atlantic-western Atlantic track, and an eastern Pacific-eastern Atlantic track. The result is a set of five general similarity statements. Cladistic biogeography goes much farther. Applying the methods of Nelson and Platnick (1981) to Rosen's poeciliid fish data it is possible to resolve 11 areas of endemism into one hierarchy. Methods of cladistic biogeography are useful for analysing and comparing biotic patterns at the highest resolution so as to compare them to independent sources of data such as geological patterns. The development of methods, such as Nelson and Platnick's assumption 2, allows generation of general biogeographic hypotheses from cladograms with seemingly ambiguous area relationships. Assumption 2 is a general empirical procedure that does not assume dispersal, vicariance, or extinction events, but, at the same time never denies that they occur (Nelson 1982; see Nelson and Ladiges 1991b,c; Humphries 1992). A cladistic view of earth history combined with cladistic procedure in systematics makes it possible to reconstruct area relationships as hierarchical relations, hence, describing area or biogeographic homology.

3

The real world

3.1 INTRODUCTION

We have established as one aim of cladistic biogeography production of area cladograms—hierarchical relationships of areas derived from cladograms of taxa. Inherent in our support for this aim is the principle that biogeographic studies must be based on sound systematics, a notion nearly universally upheld by other biogeographers (e.g. Darlington 1957, 1965; Croizat 1964; Good 1964; Brundin 1966; Rosen 1976; Nelson and Platnick 1981; Vari and Weitzman 1990; Brooks and McLennan 1991). Where vicariance and cladistic biogeographers diverge most significantly from dispersalist biogeographers is in the conviction that schemes of relationship of taxa (cladograms) within a biota are basic and fundamental to any biogeographic study, rather than are, for example, hypotheses of dispersal capabilities (vagility) of individual taxa, or estimates of centres of origin (e.g. Briggs 1984, 1986, 1995).

Examination of cladograms of different taxa from the same 'areas of endemism' for the same area relationships constitutes a search for a biogeographic pattern. These patterns are what need to be explained in historical biogeographic studies. A closer relationship of a taxon in area A to a taxon in area B than to one in area C (Fig. 3.1a) in, for example, nine independent cases is a biogeographic pattern. The pattern specifies a corroborated set of relationships among areas A, B, and C. We may look for an explanation of the pattern in geological histories of areas A, B, and C, such as separation of land mass C from A and B before separation of land masses A and B. A single exception to this pattern (Fig. 3.1b) in which a taxon in area B is more closely related to a taxon in area C than to a taxon in area A is an alternative pattern, yet does not necessarily demand a general explanation. By definition, a general explanation is applied to more than one phenomenon or, here, to more than one area cladogram. The pattern of Fig. 3.1b may be explained as an individual, random dispersal, or pattern of a different age. Such an explanation would be unique to the taxon, not to the biota, unless random dispersal were the rule. The conflicting pattern might also mean that area B is a hybrid or composite area and should be treated

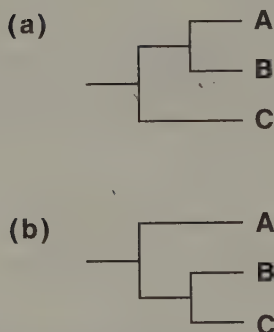


Fig. 3.1 Two hypothetical cladograms of three taxa or areas.

as two areas rather than one (see, for example, Cracraft 1989; Parenti 1991).

Not all cladistic analyses of taxa in a particular biota will yield area cladograms as straightforward as those in the above example; that is, nine taxa having one set of relationships, and one taxon having another. In Chapter 2, we considered the principal theoretical developments that led to recognition of patterns in cladistic biogeography, and methods that have been suggested to derive patterns of areas from cladograms of taxa. In this chapter, we consider what constitutes a pattern, what constitutes a conflicting pattern, and what sorts of explanations one can propose for these patterns. We consider competing geological and ecological explanations, as well as differences in estimation of relative ages of taxa. We also consider what predictions a distribution pattern for a biota allows us to make about cladistic relationships of unstudied taxa.

Thus, the question we address in this chapter is: When looking at the real world, what does a cladistic biogeographer do? We choose two problems in biogeography to apply the methodology: relationships of taxa in the North Atlantic, and relationships of North American taxa that are part of the holarctic or boreal zone biota. In the first example, our only constraint in choosing groups to include in our analysis is that a cladistic hypothesis involving three or more taxa is available. In the second example, we examine a set of cladograms for North American taxa involved in holarctic relationships to derive historical information about the temperate North American biota.

The present-day distribution of plants and animals has been caused by a variety of phenomena: geological history, climate, extinction, individual dispersal, and introduction, to name but five obvious factors. The last of these factors, introduction, is significantly different from the other four in our list because it represents a known or suspected recorded event affecting

a distribution pattern. Such distributions are of little interest to us because they require no hypotheses of explanation. For example, we need not consider here eucalypts of California because they are a known introduction of a group endemic to Australasia. If we did not know that eucalypts had been introduced into North America, their distribution might intrigue us.

The other factors in our list, for example climate (in its various manifestations, such as glaciation and rise in sea level), obviously change distribution patterns over time. But, we do not know precisely what effect they have had, or how different their effects have been on different groups of plants and animals. For example, if a taxon did not exist in North America during Pleistocene glaciation, we would not expect its distribution pattern necessarily to resemble patterns inferred from data on glacial pathways. We may conclude, however, that the pattern is at least as old as the Pleistocene if the taxon, suspected not to exist at the time of glaciation because it has only post-Pleistocene fossils, had the same distribution pattern as other taxa in a general pattern of distribution concordant with glacial pathways. We may also suspect that we have underestimated the age of our first taxon as fossils give only a minimum age of that taxon.

Thus, we emphasize importance of cladistic methods for pattern analysis, for only with area cladograms can we ask if a group conforms to a general explanation derived from distribution patterns of other groups. Area cladograms are the most resolved summaries of relationships of areas for those groups for which we have reliable phylogenetic data. It is necessary, in searching for an explanation of the distributional history of a biota, to construct and compare cladograms of taxa to find biogeographic patterns. Distributions that do not fit a general pattern have usually been explained, by vicariance and cladistic biogeographers, as random dispersals (e.g. Croizat *et al.* 1974; Rosen 1976, 1978; Nelson and Platnick 1981; Brooks and McLennan 1991). Such incongruent patterns could equally have been caused by more complex geological histories or more recent ecological factors (Savage 1982; Cracraft 1989; Craw 1989a; Parenti 1989, 1991). All of vicariance biogeography and cladistic analysis was challenged by Endler (1982), who claimed that concordance among cladograms indicates 'shared environmental effects' (p. 449), not 'history'. As we use more disparate groups in cladistic biogeographic studies, such as plants and animals, marine, freshwater, and terrestrial organisms, the chance of finding the same pattern caused principally by environmental or ecological factors rather than phylogenetic history diminishes. Later in this chapter, we address some problems in interpreting distribution patterns as resulting from specific environmental or historical factors.

We maintain that all biogeographic studies must have at their core an historical biogeographic analysis. Initially, all taxa are treated equally and

their area cladograms are combined into a general distribution pattern. Assumptions about age of groups or their present or previous dispersal ability or activity have no place in deriving a general pattern, for it is precisely these assumptions we wish to test. We shall develop some of these arguments by examining North Atlantic distributions, and then relationships of North American taxa to others in the boreal zone.

3.2 SAME PATTERN: DIFFERENT TAXA

Cladistic analyses for most North Atlantic taxa do not exist—a situation faced for almost any area of the world we may wish to look at in detail. We choose the North Atlantic as a study area because it has figured recently in cladistic biogeographic analyses (de Weerd 1989; Ho 1990; Grant and Leslie 1993). Nothing about theory and methodology of cladistic biogeography requires that its application be limited to terrestrial or freshwater organisms; cladistic biogeography applies equally well to marine life (see Croizat 1964; Brooks *et al.* 1981; Nelson 1986; Craw and Page 1988; Parenti 1991).

3.2.1 Congruence

We examine available cladograms to see what North Atlantic distribution patterns exist. Degree of congruence among cladograms of taxa from areas of endemism throughout the North Atlantic is the extent to which they agree. De Weerd (1989) published a pioneering study in which she described marine areas of endemism for chalinid sponges and analysed area relationships in the North Atlantic, using cladistic methodology. We use her analysis as a starting point in a search for congruence among area cladograms.

Six areas of endemism were described for North Atlantic chalinid sponges (Fig. 3.2): area 1, Arctic; area 2, boreal; area 3, Mediterranean; area 4, south-eastern North Atlantic; area 5, western North Atlantic; and area 6, Caribbean (de Weerd 1989). (A seventh area, the Netherlands, was described for some taxa, but de Weerd eliminated this area from her general area cladogram, as do we.) Specifying relationships among these areas is not necessarily a small task: there are 2752 possible rooted trees, including 945 completely dichotomous trees, for six taxa or areas (Felsenstein 1978).

Seven cladograms of taxa and areas were presented for eight chalinid species groups classified in three genera, *Acervochalina*, *Dendroxea*, and *Haliclona* (de Weerd 1989, fig. 12 a–g). Using assumption 0 (see Chapter 2) to generate possible area relationships, de Weerd (1989, p. 79) combined



Fig. 3.2 Areas of endemism for chalinid sponges in the North Atlantic (after de Weerd 1989, Fig. 11): area 1, Arctic; area 2, boreal; area 3, Mediterranean; area 4, south-eastern North Atlantic; area 5, western North Atlantic; area 6, Caribbean.

components from the seven cladograms to yield 19 alternative area cladograms (Table 3.1). In other words, de Weerd proposed that of the possible cladograms for six areas, 19 are specified, in whole or in part, by some group of chalinid sponges under assumption 0. The strict consensus tree among these 19 cladograms is completely unresolved (Fig. 3.3a). We do not accept a strict consensus tree as a useful summary of area relationships because it is no better than choosing any one of 2752 possible cladograms, or one of the 945 dichotomous cladograms; after all, de Weerd's analysis reduced the possible number to just 19 of these.

De Weerd chose the most parsimonious summary of these area cladograms calculated by the program *CAFCA* (Zandee 1987) as a general area cladogram (Fig. 3.3b). We also calculated the Nelson consensus tree (Fig. 3.3c) using *COMPONENT* 1.5 (Page 1989a). The Nelson consensus tree summarizes the repeated, uncontradicted components among the 19 trees. In contrast to the strict consensus tree (Fig. 3.3a), these two area cladograms (Fig. 3.3b,c) have greater resolution, and agree that areas 3 and 4 are sister areas, and that area 5 is plesiomorphic. They differ in placement of areas 2 and 6.

What is the general area cladogram that specifies relationships among

Table 3.1 Nineteen possible area cladograms for six species groups of North Atlantic chalinid sponges (from de Weerd 1989, p. 79)

1.	(((1, 2), 5), 3), 6), 4)
2.	(((1, 2), 5), 3), 4), 6)
3.	(((2, 3), 4), 6), 5), 1)
4.	(((2, 3), 5), 1), 6), 4)
5.	(((2, 3), 5), 1), 4), 6)
6.	(((3, 4), 1), 2), 6), 5)
7.	(((3, 4), 1), 6), 2), 5)
8.	(((3, 4), 2), 6), 1), 5)
9.	(((3, 4), 5), 6), 2), 1)
10.	(((3, 4), 5), 2), 6), 1)
11.	(((3, 4), 6), 2), 1), 5)
12.	(((2, 5), 1), 3), 4), 6)
13.	(((2, 5), 1), 3), 6), 4)
14.	(((3, 6), 4), 1), 2), 5)
15.	(((3, 6), 4), 2), 1), 5)
16.	(((1, 2), (3, 4), 6), 5)
17.	(((1, 2), (3, 6), 4), 5)
18.	(((3, 4), (2, 5), 6), 1)
19.	(((2, 5), (3, 6), 4), 1)

the six areas of endemism? Remember from Chapter 2 that we recognize two steps in an historical biogeographic analysis: enumerating all possible area relationships allowed by our species cladogram and species distributions, and summarizing possible area relationships. In Chapter 2, we outlined reasons for advocating assumption 2 (Nelson and Platnick 1981) to generate area cladograms from taxon/distribution cladograms. We use assumption 2 to illustrate how a general pattern might be constructed from chalinid species/area cladograms that include all six areas of endemism (Fig. 3.4a,b).

The nine species in the *oculata* group (genus *Haliclona*) and the eight species in the *rosea* group (called the *rosea* and *dendroxea* group by de Weerd; comprising species in the genera *Haliclona* and *Dendroxea*, respectively) are distributed in all six areas of endemism as specified by the cladograms of Fig. 3.4a and b, respectively. Under assumption 2, *COMPONENT* 1.5 built 52 dichotomous area cladograms for the *oculata* group and two for the *rosea* group; 54 possible area cladograms in total (Table 3.2). These area cladograms could be figured by hand; obviously, a computer makes our task much easier. Fifty-four possible area cladograms for the six areas are produced using assumption 2 compared with 19

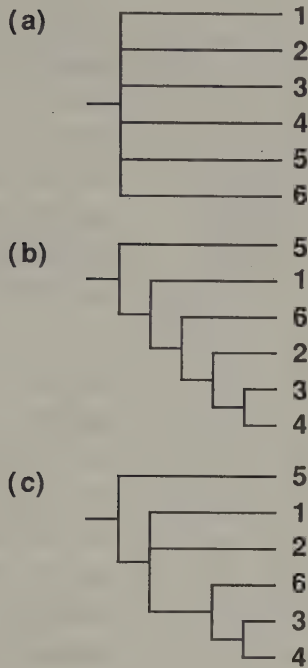


Fig. 3.3 Three possible summaries of 19 area cladograms in Table 3.1: (a) strict consensus tree; (b) summary from de Weerd (1989, Fig. 13) using *CAECA*; (c) Nelson consensus tree.

possible area cladograms found by de Weerd using assumption 0 (Table 3.1). The 35 additional area cladograms include 20 in which areas 1 and 5 are sister areas (Table 3.2).

There are no shared trees or intersections between the set of 52 area cladograms for the *oculata* group and the two for the *rosea* group (Table 3.2). This conclusion can be identified in de Weerd's (1989) analysis also. For example, parts of the species/area cladogram for the *oculata* group do not fit her general area cladogram (see de Weerd 1989, p. 83). The two groups either have no shared history, or, more likely, they express different parts of a redundant or repeated pattern (Page 1989a,b). At the minimum, we may ask: What components of area relationships are repeated and not contradicted between the two species groups? The Nelson consensus tree for the 54 area cladograms, calculated using *COMPONENT* 1.5, is completely resolved (Fig. 3.5). As we might expect, it includes areas 1 and 5 as sister areas.

Not all species in each group occur in all six areas of endemism. Species groups with missing areas can give us no information on relationships of

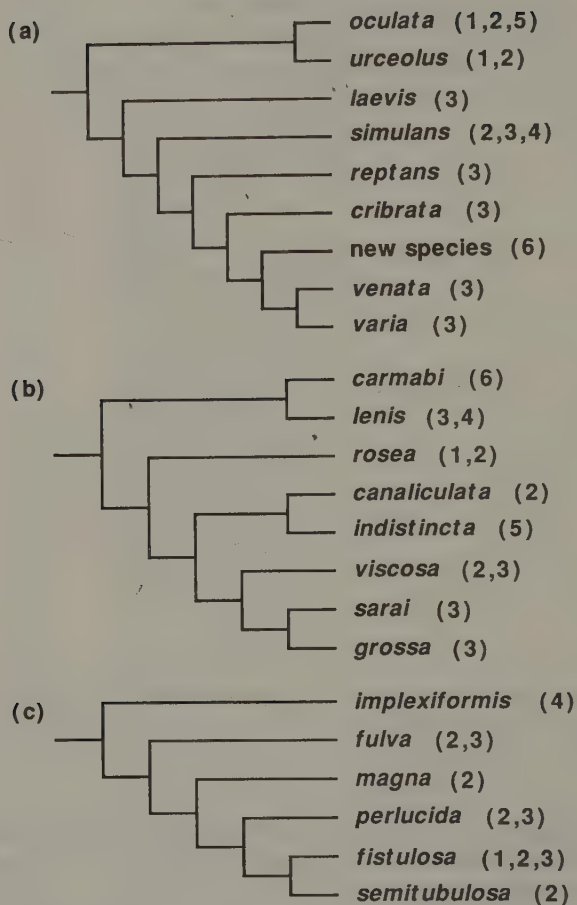


Fig. 3.4 Area cladograms of four chalinid species groups (from de Weerd 1989, fig. 12). Numbers in parentheses are areas of endemism occupied by the species: (a) *oculata* group (fig. 12a); (b) *rosea* group, combined with *Dendroxea* group (fig. 12c); (c) *fistulosa* group (fig. 12d).

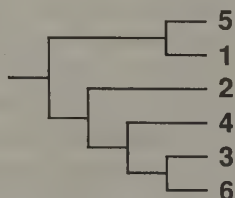


Fig. 3.5 General area cladogram summarizing area relationships for chalinid sponges of Fig. 3.4a and b.

Table 3.2 Fifty-four possible area cladograms for six areas as specified by chalinid sponges (Fig. 3.4a,b), under assumption 2

52 Cladograms for the <i>oculata</i> group		29.	((1, 2), (((3, 5), 6), 4))
1.	((((1, 3), 6), 4), (2, 5))	30.	((1, 2), (((3, 6), 4), 5))
2.	((((1, 4), 6), 3), (2, 5))	31.	((1, 2), (((3, 6), 5), 4))
3.	((((1, 6), 3), 4), (2, 5))	32.	((1, 2), ((3, (4, 6)), 5))
4.	((((1, 6), 4), 3), (2, 5))	33.	((1, 2), ((3, (5, 6)), 4))
5.	((1, (3, 6)), 4), (2, 5))	34.	((1, 2), ((3, 5), (4, 6)))
6.	((1, (4, 6)), 3), (2, 5))	35.	((1, 2), ((3, 6), (4, 5)))
7.	((1, 2), ((3, 6), 4)), 5)	36.	((1, 2), (3, ((4, 5), 6)))
8.	((1, 2), (3, (4, 6))), 5)	37.	((1, 2), (3, ((4, 6), 5)))
9.	((1, 2), 5), ((3, 6), 4))	38.	((1, 2), (3, (4, (5, 6))))
10.	((1, 2), 5), (3, (4, 6)))	39.	((1, 5), (((2, 3), 6), 4))
11.	((1, 3), (4, 6)), (2, 5))	40.	((1, 5), (((2, 4), 6), 3))
12.	((1, 4), (3, 6)), (2, 5))	41.	((1, 5), (((2, 6), 3), 4))
13.	((1, 4), 5), ((2, 6), 3))	42.	((1, 5), (((2, 6), 4), 3))
14.	((1, 4), 5), (2, (3, 6)))	43.	((1, 5), ((2, (3, 6)), 4))
15.	((1, 5), ((2, 6), 3)), 4)	44.	((1, 5), ((2, (4, 6)), 3))
16.	((1, 5), ((3, 6), 4)), 2)	45.	((1, 5), ((2, 3), (4, 6)))
17.	((1, 5), (2, (3, 6))), 4)	46.	((1, 5), ((2, 4), (3, 6)))
18.	((1, 5), (3, (4, 6))), 2)	47.	((1, 5), ((2, 6), (3, 4)))
19.	((1, 5), 2), ((3, 6), 4))	48.	((1, 5), (2, ((3, 4), 6)))
20.	((1, 5), 2), (3, (4, 6)))	49.	((1, 5), (2, ((3, 6), 4)))
21.	((1, 5), 4), ((2, 6), 3))	50.	((1, 5), (2, (3, (4, 6))))
22.	((1, 5), 4), (2, (3, 6)))	51.	(1, ((2, 5), ((3, 6), 4)))
23.	((1, ((3, 6), 4)), (2, 5))	52.	(1, ((2, 5), (3, (4, 6))))
24.	((1, (2, 5)), ((3, 6), 4))	2 Cladograms for the <i>rosea</i> group	
25.	((1, (2, 5)), (3, (4, 6)))	53.	((1, ((2, 3), 5)), (4, 6))
26.	((1, (3, (4, 6))), (2, 5))	54.	((1, ((2, 5), 3)), (4, 6))
27.	((1, (4, 5)), ((2, 6), 3))		
28.	((1, (4, 5)), (2, (3, 6)))		

missing areas (see Chapter 2). The *fistulosa* group has species in areas 2, 3, 4, and 6, but not areas 1 or 5 (Fig. 3.4c). There are two possible area cladograms specified by the *fistulosa* group (Fig. 3.6a,b) under assumption 2. The strict and Nelson consensus trees between Fig. 3.6a and 3.6b are identical (Fig. 3.6c). All three area cladograms (Fig. 3.6) differ from general area summary (Fig. 3.5) in relationships for areas 2, 3, 4, and 6. Is something wrong? No, because missing from the area relationships specified by the *fistulosa* group is the relationship of area 2 to areas 1 and 5. Area cladograms for the *oculata* and the *rosea* groups specify a close relationship between areas 5 and 2 (Fig. 3.4b), or among areas 1, 2,

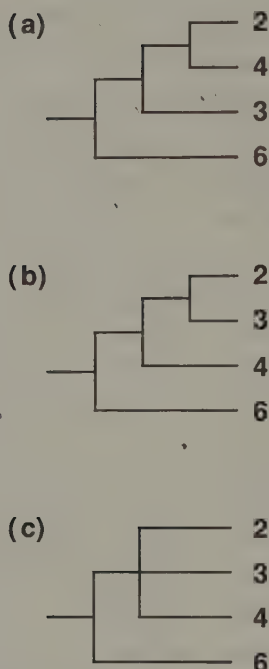


Fig. 3.6 (a,b) Two possible area cladograms for the *fistulosa* group (Fig. 3.4c). (c) Strict or Nelson consensus of a and b.

and 5 (Fig. 3.4a), and these relationships are reflected in the general area summary (Fig. 3.5).

To ask if this biogeographic pattern is unique to sponges or has some general significance, we examine additional cladograms of North Atlantic taxa. Merlucciid hakes are one of several gadiform fish families that have bipolar or antitropical distributions (Ho 1990; Howes 1990). Ho (1990) summarized results of a phylogenetic and biogeographic analysis of the bipolar, coastal *Merluccius* in a taxon/area cladogram (Fig. 3.7). Merlucciid hakes are more widespread than chalinid sponges; yet, both groups are coincident in the North Atlantic. Distribution of Pacific and southern Atlantic hakes can neither agree nor disagree with the general pattern. Plesiomorphic merlucciids inhabit the western North Atlantic (approximately areas 5 and 1; Fig. 3.2). More derived merlucciids inhabit the eastern North Atlantic (approximately area 2; Fig. 3.2). So, even though merlucciid hakes and chalinid sponges are distantly related taxa with different overall distributions, where distribution patterns overlap, they agree. A better test of the chalinid sponge area relationships is possible by including another taxon with representatives found in each of the six North Atlantic areas of

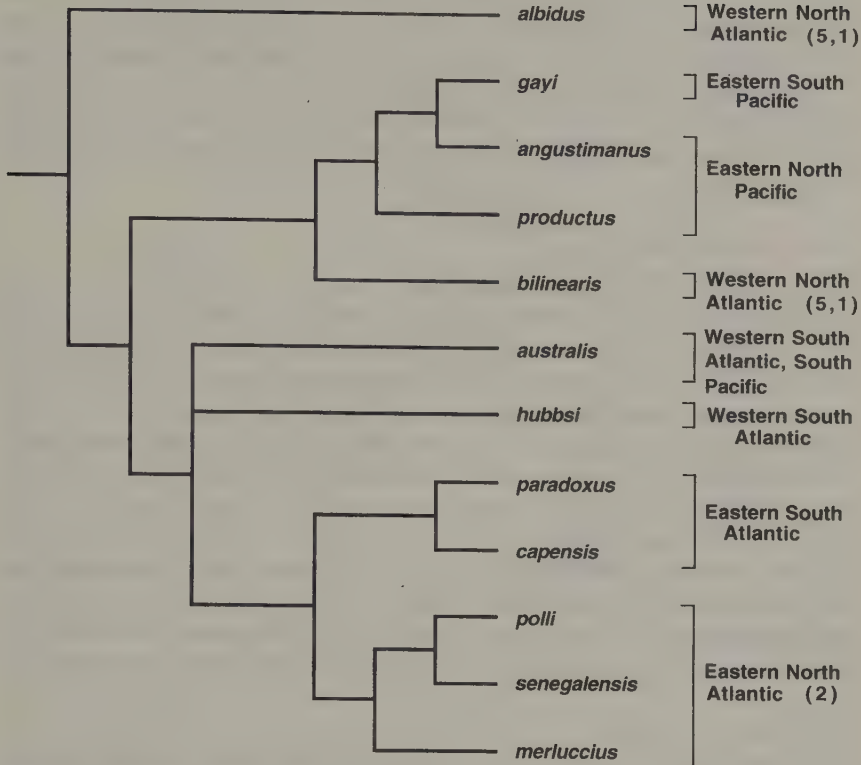


Fig. 3.7 Cladogram of hake species, genus *Merluccius*, and their distribution (after Ho 1990, Fig. 7).

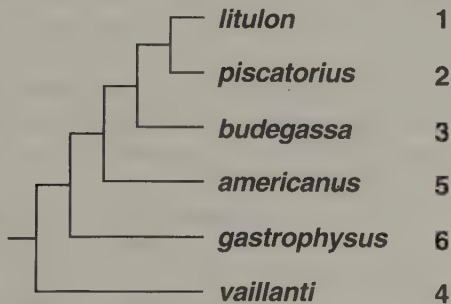


Fig. 3.8 Taxa and area cladogram for northern species of the anglerfish genus *Lophius* (following Grant and Leslie 1993). Areas are numbered as in Fig. 3.2.2; *L. litulon*, from the northern Pacific, is treated broadly here as an Arctic species (see Grant and Leslie 1993, figs 1, 5). A seventh species of uncertain relationship, *L. vomerinus*, from the southern Atlantic, has been omitted here.

endemism. Grant and Leslie (1993) provide an area cladogram for the anglerfish genus *Lophius* (Fig. 3.8), an unambiguous statement on the relationships among areas 1 through 6. We analyse relationships among the six areas for the two chalinid groups (*oculata*, *rosea*), and *Lophius*, under assumption 2 using *COMPONENT* 2.0 (Page 1993a) and *TAS/TASS* (Nelson and Ladiges 1991c,d, 1993, 1994, 1995 and personal communication).

3.2.1.1 *COMPONENT* 2.0

Using *COMPONENT* 2.0, we explore biogeographic relationships within the Atlantic ocean as determined from the three data sets (Table 3.3). The *oculata* group alone is completely uninformative, giving all 945 possible area cladograms for 6 areas. The problems of widespread taxa are most apparent for sponges, giving at least one third of all possible trees when using the standard option in *COMPONENT* 2.0, for both the *rosea* group and the *rosea* and *oculata* groups combined. This means that what little structure there is when using only the sponge taxa comes from the *rosea* group. The Nelson consensus tree, (6(1, 2, 5(3, 4))), has two resolved nodes suggesting that the Mediterranean and south-eastern North Atlantic areas have sister group relationships, and are nested within the northern and north-western areas. Under assumption 2, 83 trees were obtained. The Nelson consensus tree suggests an unusual sequence of: (1,(4,(5,(2,(3, 6)))))

Lophius has a unique pattern that dominates the combined analysis under assumption 2 (see Fig. 3.9). The solution indicates that if there is a history common to all three taxa, then the boreal and Arctic areas, broadly defined, are nested sequentially within areas of warmer waters. Perhaps the most surprising result is that the Mediterranean sea is most closely related to northern waters, rather than to the Caribbean, for example.

Table 3.3 *COMPONENT* 2.0 analyses of the *oculata* and *rosea* groups of sponges and *Lophius*. The 'subtree, pruning-regrafting' option was used

	Number of trees obtained	
	No assumption	Assumption 2
<i>oculata</i> group	945	945
<i>rosea</i> group	315	3
<i>Lophius</i>	1	1
<i>oculata</i> + <i>rosea</i> groups	315	83
<i>oculata</i> + <i>rosea</i> + <i>Lophius</i>	8	1

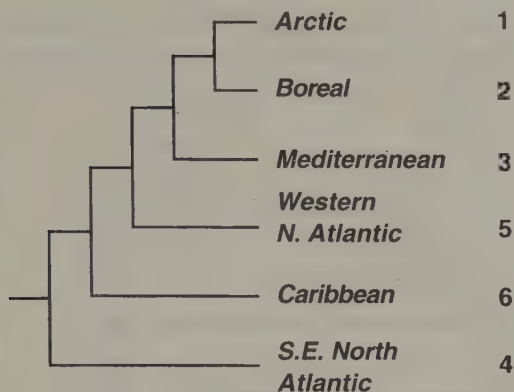


Fig. 3.9 Area cladogram for six areas of endemism calculated under assumption 2 on combined data set for *oculata/rosea/Lophius* analysed using *COMPONENT 2.0*.

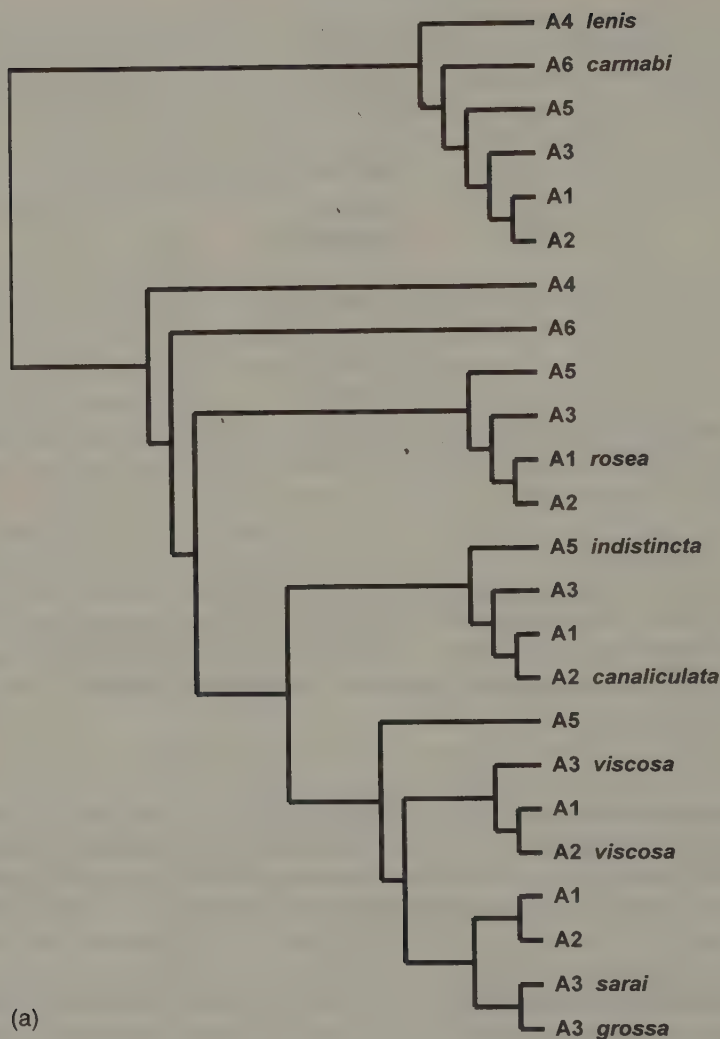
The reconciled trees are shown in Fig. 3.10. We conclude that both groups of sponges have complex distributional histories. Because of considerable redundancy for areas 2 and 3 and widespread distributions in several taxa, the biogeographic signal is opaque compared with the resolved *Lophius* pattern.

3.2.1.2 TAS/TASS

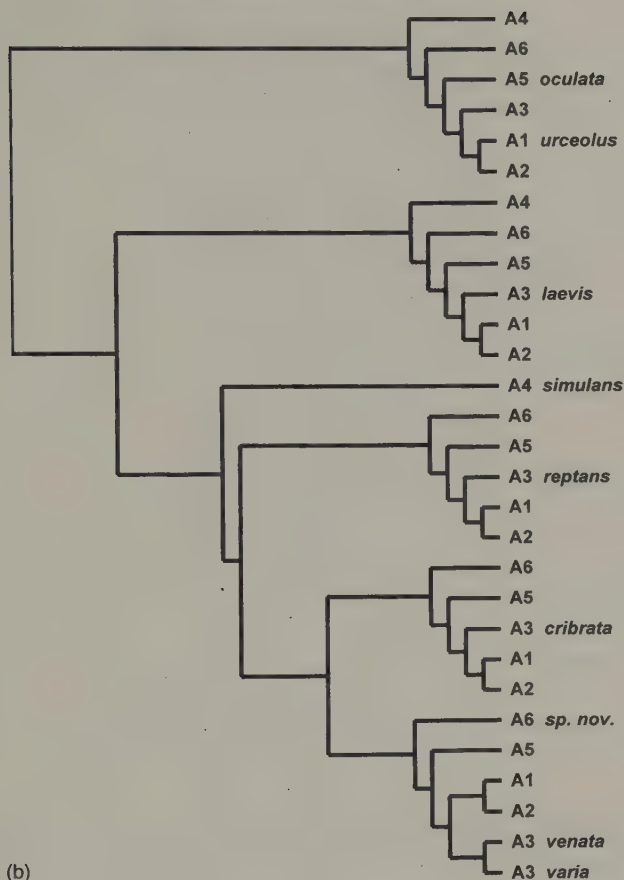
Similar analyses were undertaken using the *TAS/TASS* programs of Nelson and Ladiges (1991d, 1994, 1995). The main purpose of our analysis was to determine precisely what informative patterns could be obtained from the three fundamental area cladograms. Under assumption 2, *TASS* yielded four informative trees (Fig. 3.11). When the four informative trees were coded into three-item statements and analysed with *TAS*, four distinct area cladograms were obtained (Fig. 3.12). Figure 3.12c is identical to the result obtained for assumption 2 with *COMPONENT 2.0* (Fig. 3.9). Inspection of the other three trees reveals that the ambiguous positions for areas 1 and 5 reflect the different positions for these areas in the two sponge cladograms, preventing a clear-cut interpretation.

3.2.2 General explanations

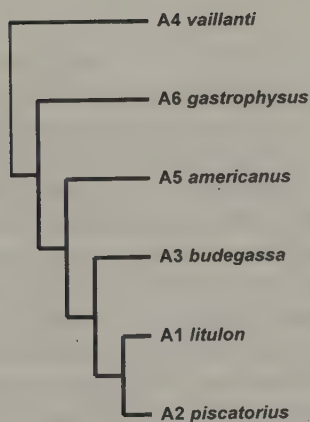
How do we explain a pattern such as Fig. 3.9? Many biogeographers maintain that distribution patterns should be explained group by group; that is, no general explanation should be sought because different taxa have different dispersal capabilities or are of different ages. The latter idea is



often allied with strict interpretations of the fossil record and reliance on the record to explain somehow historical distributions. It has been assumed that groups of plants and animals arose in different epochs and dispersed around the world as and when each could. For animal groups, the Palaeozoic and Mesozoic periods are traditionally the Age of Fish, then of Reptiles, respectively. The Cenozoic is the Age of Mammals. This hypothesis of spread of plants and animals over the world is also tied to ideas about a stable earth as exemplified by George's statement 'But it seems easier to



(b)



(c)

Fig. 3.10 Reconciliation trees for (a) *rosea*, (b) *oculata*, and (c) *Lophius*, mapped on to the area tree of Fig. 3.9.

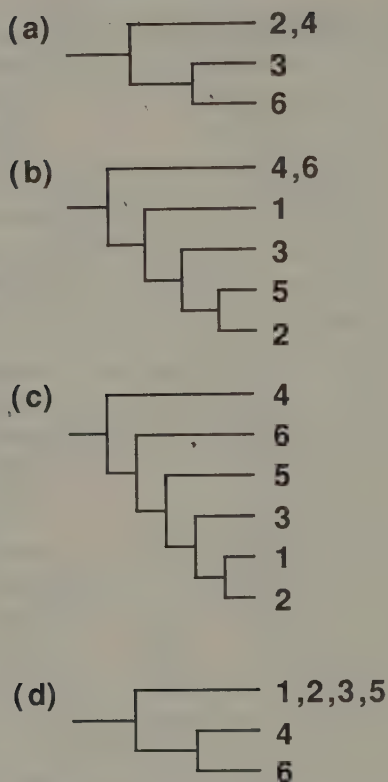


Fig. 3.11 Four informative area cladograms (a–d) obtained for *oculata*, *rosea*, and *Lophius* using TASS.

make animals move round the world and fill permanent continents than to make the continents move round to collect them' (George 1962, p. 96).

During the past three decades incorporation of almost universally accepted ideas of a changing geography has altered traditional explanations for particular plant and animal distributions. Speculation about ages of taxa relies on assumptions that groups are at least as old as their oldest fossil representatives. Some biogeographers have emphasized that a fossil gives only the minimum age of a group (e.g. Croizat 1964; Patterson 1981a; Grande 1985), but this idea has yet to be fully incorporated into biogeographic studies. Lundberg (1993) used fossil evidence to show that some fish taxa are older and some are younger than the timing of a proposed split between South America and Africa. Lack of sufficiently old fossil representatives of cichlid and cyprinodontiform fishes convinced

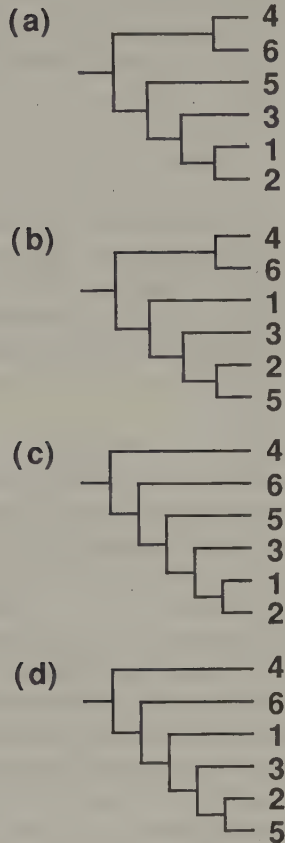


Fig. 3.12 Four informative area cladograms (a–d) for *oculata*, *rosea*, and *Lophius* obtained using *TAS* and *Hennig86*.

him that dispersal must have played a significant role in the distribution of these two wide-ranging taxa (see also Chapter 2).

Dispersal need not be an *a priori* assumption of the cause of a particular distribution, and present distribution patterns need not have been caused by relatively recent (Quaternary) climatic events (see Rosen 1976). Heads (1990) argues that patterns of earth history and biogeography suggest that the world today reflects a large-scale renovation that took place during the Upper Mesozoic. Parts of distribution patterns undoubtedly have been caused by relatively recent and chance events, yet a common, underlying pattern for several groups inhabiting the same areas requires a general explanation.

What then can we say about the pattern of Fig. 3.9? What sort of general

explanation could fit different groups? What would such an explanation mean? What would one use it for?

An explanation for the pattern in Fig. 3.9 may include the following considerations:

- There are repeated trans-Atlantic relationships. Area 5, western North Atlantic, is sister to areas 3, 2, and 1, and area 4, south-eastern North Atlantic, is sister to all remaining areas.
- Proximity does not dictate area (or taxon) relationship. Area 5, western North Atlantic, and area 6, Caribbean, are closer to each other geographically than either area is to any third area of endemism. However, they are not sister areas in any summary of area relationships (Figs 3.3b, 3.5, 3.9).

3.2.3 Predictions

Having recognized one general pattern, we consider which predictions we can test in future studies. Predictions may concern at least four topics: cladograms of taxa, cladograms of areas, geological hypotheses supported by patterns, and ages of biotas.

The first two predictions, cladograms of taxa and areas, are intimately related. We predict that taxa found in the North Atlantic are related in a manner that yields an area cladogram congruent with Fig. 3.9; that is, we predict that additional taxa will not conflict with the pattern. In this way, we test one important aspect of our pattern: does the general explanation really help to describe the history of a region (here, the North Atlantic), or is it unique to some fishes and sponges, and therefore irrelevant to other members of the North Atlantic biota? We emphasize that relationships of taxa in endemic areas are predicted at any taxonomic level. It is not instructive to restrict ourselves to comparing relationships of, for example, genera or families of sponges, fish, and so on, because ranks of such taxonomic categories are arbitrary and incomparable across phyletic lines.

Corroboration of the general pattern by more taxa would support our interpretation of the relationships of the areas. Plants and animals that share a cladistic pattern share a history. Implicit in this statement is the concept that all groups sharing the pattern are of approximately the same age, or at least all as old as the first vicariant event that formed the pattern, otherwise, they could not all have responded to the same events at the same time. Fossils help to reject geological explanations for a particular pattern (see Section 3.3.2). Most taxa, such as chalinid sponges, have no fossil representatives. Of those that do, fossils may be relatively young. A fossil merlucciid hake, *Merluccius inferus*, is known from the middle Oligocene of Europe (Ho 1990). Using fossil evidence alone, we can estimate the mini-

minimum age of hakes as middle Oligocene; we have no direct evidence for the age of chalinid sponges other than Recent, although demosponges as a group date from the Cambrian (de Weerd 1989).

If one or several groups showing the pattern of Fig. 3.9 had early Mesozoic (Jurassic/Triassic) fossil representatives, we could come to either one of two conclusions:

- (1) the pattern is at least as old as the early Mesozoic and we have underestimated minimum ages of other taxa; or
- (2) the group with early Mesozoic representatives remained unaffected by any postulated vicariance events until the Cretaceous, by which time other taxa had evolved, became sympatric with it, and all were affected together by subsequent vicariance events.

An explanation for our general pattern might not be found in prevailing geologic theory, but we can look for correlation of geologic events with the pattern, particularly its trans-Atlantic components (Fig. 3.9). King (1983) estimated that Laurasia and Gondwanaland began their latest episode of rifting in mid-Jurassic times (approximately 180 million years ago), opening the modern Atlantic ocean. We may estimate the minimum age of the ancestral North Atlantic biota to be mid-Jurassic. Subsequent divisions in the general pattern (between the Mediterranean (area 3) and the boreal (area 2) and Arctic (area 1) regions) occurred later. Thus, not all 'trans-Atlantic' patterns are the same age (Bremer 1993), but a hierarchy of relative ages may be inferred from the general area cladogram.

3.2.4 Redundancy

There is redundancy in Ho's (1990) hake cladogram; the same areas (such as western North Atlantic) appear more than once. Is this a conflict with the general pattern of Fig. 3.9? No. Biogeographic patterns repeat (Croizat 1964; Nelson and Platnick 1981) within, as well as between, taxonomic groups. Consider the widespread, freshwater and marine, labroid fishes (see Stiassny and Jensen 1987; Fig. 3.13). The labroid area cladogram repeats, from plesiomorphic to apomorphic taxa: pantropical freshwater (Cichlidae), boreal marine and occasionally freshwater Pacific (Embiotocidae), pantropical marine (Pomacentridae), bipolar and pantropical marine (Labridae). That some labroids are freshwater and others marine is irrelevant to formation of the repeated pattern. What is notable about labroids is that embiotocids are not bipolar, but restricted to the Northern Pacific. One prediction we might make is that southern hemisphere embiotocids, or their sister group (as fossil or Recent taxa), may be discovered.

Cladograms of areas for three fish groups, paddlefishes, bowfins, and umbrids (mud-minnows), are shown in Fig. 3.14. These are all modified from Patterson (1981b), which he derived from published information. The cladogram for umbrids includes two positions for the genus *Dallia* of Alaska and eastern Siberia, represented by two broken lines; relationships of umbrids are unresolved.

The different areas are treated, for discussion, as four areas: western North America (including Alaska), eastern North America (including south-eastern North America and central North America), Europe, and Asia (including eastern Siberia).

When both eastern North America and Europe appear together on a cladogram, they may be sister groups (Fig. 3.14b for recent umbrids). A conflict arises when trying to decide which area, Asia or western North America, is most closely related to them. In bowfins (Fig. 3.14c) the answer is clearly western North America; for paddlefishes the answer is Asia. The position of umbrids is unresolved.

We see a problem in summarizing clearly relationships among the four areas. In fact, information from the cladograms of Fig. 3.14 is best summarized by the cladogram of Fig. 3.15a; that is, there is an unresolved trichotomy among Asia, western North America, and eastern North America–Europe.

There is more evidence on relationships of these three areas that can help us resolve the problem. Grande (1985) examined relationships of Green River Eocene fishes, and found that the general pattern is for western North American taxa to be more closely related to Asian (or other trans-Pacific) taxa than to eastern North American or European taxa (see also Grande 1994). Thus, a resolution of the area cladogram of Fig. 3.15a is presented in Fig. 3.15b in which Asia and western North America form sister areas that, together, are most closely related to an eastern North American–European sister area pair.

Consider four possible explanations for this pattern:

1. Phylogenetic relationships proposed for some groups is wrong, and all North American taxa form a monophyletic group that is either most closely related to Asian or to European taxa.
2. One group of taxa was influenced primarily by vicariance events affecting that section of the North American biota, whereas other North American taxa dispersed.
3. The two patterns reflect a real, separate history of western and eastern North America.
4. The two patterns reflect an older and a younger biotic component, the older pattern caused by older vicariance events, the younger pattern by more recent events.

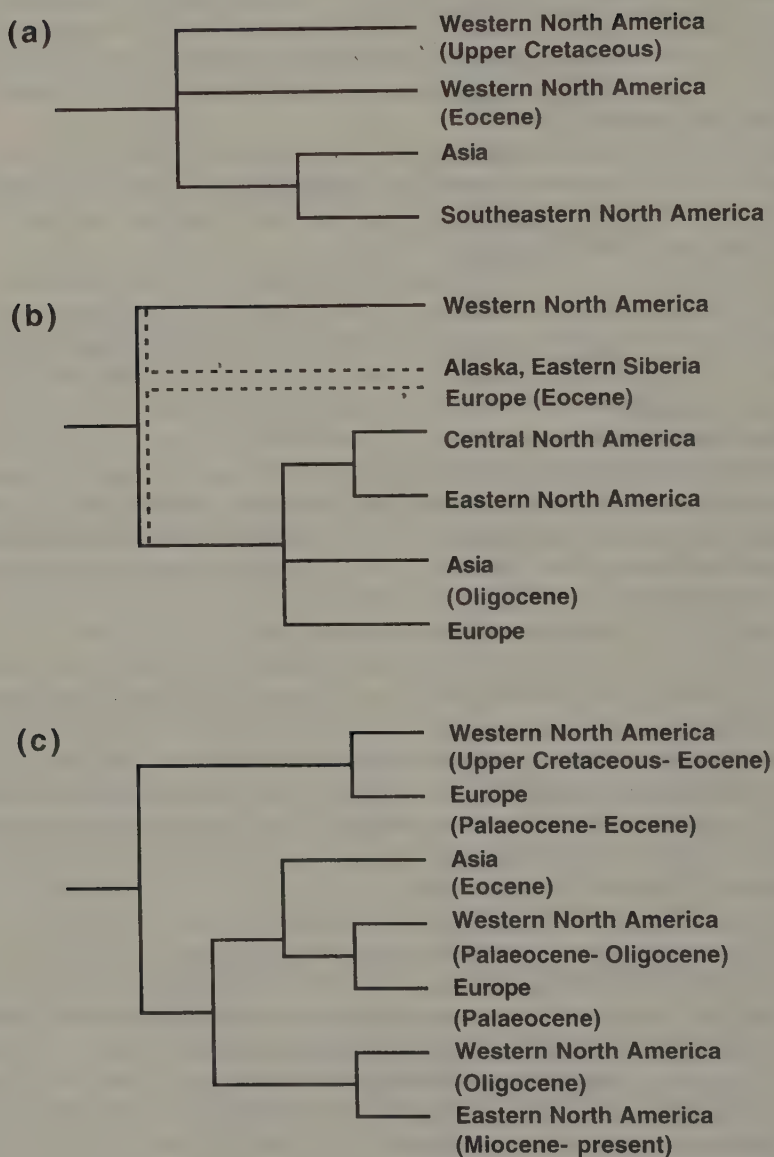


Fig. 3.14 Area cladograms with ages of fossil representatives for (a) paddlefishes, (b) umbrids, and (c) bowfins. (Modified from Patterson 1981b.)



Fig. 3.15 (a) General pattern of area relationships derived from cladograms of Fig. 3.14. (b) General pattern of Fig. 3.14a with position of western North America resolved.

The first explanation, erroneous phylogeny, is always possible, but can only be confirmed with additional characters or taxa. Therefore, we consider the two positions for North America in Fig. 3.15b to be real, and seek an explanation among the three other possibilities.

The second possibility, that one pattern for North America is explained by dispersal and the other by a set of vicariance events that affected all taxa in another part of the continent, is contrary to what we predict about patterns; that is, that they have general explanations. Therefore, we are left with two possibilities for an explanation of the 'biphyletic' nature of the North American biota, which we discuss separately.

3.3.1 Areas of hybrid origin

The decision to treat North America as two regions, an eastern and a western, reflects relationships of the North American fish fauna. Division of the continent, however, is not obvious because where it may be divided, based on recent distributions, differs from taxon to taxon. For example, umbrids of western North America are confined to Washington State, whereas Green River Eocene fishes are distributed throughout Wyoming, Utah, and Colorado. Thus, when we say that western North America is an area distinct from eastern North America we are referring to an imprecise division of the modern continent. The pattern of Fig. 3.15b implies a separate history of the two areas, western North America shares a component of its history with Asia rather than with eastern North America,

which shares a component of its history with Europe (Croizat 1961). Because what we call North America is now, and for a long time has been, one continent, these 'basic components' of history, if they reflect independent geological histories of western and eastern North America, suggest that the modern continent was two or more separate areas in the distant past.

Geological evidence that North America was at one time separated into two or more areas supports the idea that the pattern of Fig. 3.15b is a direct result of the continent's geological history. The idea is not original to us; it has been hypothesized that Asia and some part of western North America once lay side by side. There are two possibilities: either the eastern and western halves of North America constitute at least two separate units fused together, or, at one time an epicontinental sea divided a single continent into two. Geological evidence suggests that growth of North America has not been gradual but episodic. According to Jones *et al.* (1982; see also Chamberlain and Lambert 1985) virtually the entire Pacific coast from Baja California in the south, north to the tip of Alaska, and extending up to 500 km inland, is a series of prefabricated blocks grafted on to the main North America block. These blocks, known as 'accreted terranes', have been carried many thousands of kilometres east and north from previous Pacific sites (see also Howell 1985; Minckley *et al.* 1986; Hamilton 1988). 'Terrane fidelity', restriction of taxa to individual terranes, has been demonstrated for bolitoglossine salamanders (Hendrickson 1986).

Second, that an epicontinental sea divided the North American continent into western and eastern components from the Upper Jurassic to the Lower Cretaceous, especially during the Upper Cretaceous and not before, or since, is geologically well established (see Howarth 1981 for review). We discuss this idea more fully in Chapter 4, but emphasize here that the biological pattern suggests different histories for western and eastern North America since these fish first existed, and also perhaps predicts what geologists will discover, rather than refutes or corroborates any one geological hypothesis that we could advance for the history of the continent.

3.3.2 Patterns of different ages

Suppose that there was no evidence for independent geological histories of western and eastern North America, or that if there were, it indicated a separation of the continent in the distant past so that we thought it could have nothing to do with the existing biological pattern. We could consider that there is an older and a younger component to the biological pattern. As a hypothetical example, consider that one group of North American

taxa, with closest relatives in Asia, had existed in western North America since the Cretaceous. Members of the taxa may have even been more widespread than they are now, and had their ranges reduced by subsequent extinction. A second group of taxa, relatively younger, in existence since the Oligocene, could be widespread in eastern North America, with closest relatives in Europe.

How viable is this explanation for our pattern? Relationships of western North American taxa with Asian taxa are at least as old as the Eocene (Fig. 3.14c). Relationships of eastern North American taxa with European taxa are at least as old as the Eocene as well, so it is impossible with Eocene data to resolve the general pattern (Fig. 3.15b) into two patterns, one older and one younger. (See Cavender 1986 for a summary of the fossil record of North American freshwater fishes.)

When we look further at ages of area associations of Fig. 3.14, we see that there is a relatively old (Upper Cretaceous to Eocene) relationship between western North America and Europe (Fig. 3.14c). This does not conflict with the general pattern of Fig. 3.15b, as we have discussed in deriving the general pattern. Nonetheless, it indicates some older association between western North America and Europe. This could mean either that there was some ancient ancestral biota that included two areas, or that in fact just part of western North America is associated with Europe and part with Asia. A decision to subdivide further North America in our biogeographic study can only be based on conflicting cladistic relationships of taxa endemic to those areas. Additional cladistic information for more North American taxa may require such a subdivision. We caution that geological evidence alone should not require subdivision of North America in a biogeographic analysis but only suggest an explanation for a biological pattern. Otherwise, we would be letting geology rather than biology dictate our regions of endemism, and that would be unsound biogeography.

These predictions, that there are older and younger components to a biogeographic pattern, need to be corroborated by additional fossil evidence. A younger pattern automatically becomes the older pattern if a fossil of greater age than that older pattern is found. Fossil evidence may vary from group to group and be a result more of vagaries of preservation and discovery than actual age of the group. According to Patterson (1981a), with whom we concur, fossils have two unique roles in cladistic biogeography. First, they document extinctions, thereby, by inclusion, extend ranges of groups allowing new areas and new test groups to be considered. Second, by giving minimum ages to groups, they ensure that comparisons between different groups are valid and permit a choice of geological events of different ages.

3.4 GEOLOGY AND THE CLADISTIC BIOGEOGRAPHER

Geological hypotheses for history of areas of endemism have influenced biogeographers, more often than not, to such an extent that they interpret biological patterns solely as a reflection of prevailing geological theory or do not consider patterns within biotas, but interpret distribution of a single taxon according to one particular geological explanation.

Geological hypotheses for histories of areas of endemism are no more or less valid than is the history of a biota inhabiting those areas as represented by a biogeographic pattern. As Croizat (e.g. 1964) repeated, biological patterns exist whether or not they agree with geology.

We assume that, on some level, histories of areas derived from biological and geological data should agree. That biological relationships and their associated area relationships should stand as evidence independent of geological relationships of areas is one tenet of cladistic biogeography. None the less, in searching for explanations of distribution patterns, biogeographers are continually intrigued and influenced by geological evidence. We consider here some ways in which geological evidence has been used in biogeographic studies, and ways in which it may help explain a pattern.

3.4.1 Cladograms of taxa

What refutes a cladogram of taxa? What evidence would make us change our hypothesis of a general phylogeny of a group? Addition of new characters, or doubt about some characters already used to construct the cladogram, but not details of geography. If a cladogram indicates that the taxon in area A is more closely related to the taxon in area B than either one is to the taxon in area C (as in, for example, Fig. 3.1a), and the prevailing geological hypothesis indicates that area B shares a history with area C but not with A (as in, for example, Fig. 3.1b), we would not conclude that geology refutes our biological analysis. Furthermore, and perhaps more important, we must always try to test a pattern in biogeography, not test individual cladograms. To begin constructing general explanations for distributions within biotas we must examine at least two, preferably more, taxa. Examining the cladogram of relationships within one taxon and comparing it to the prevailing geological hypothesis is analogous to trying to decide, using an organism's vagility, whether or not its distribution is the direct result of random dispersal. It is a fruitless 'test' of a pattern where no pattern may exist.

For example, consider an example in which geology of a region is fairly well-known, or even in which recent geological events are known with certainty because they have occurred within recorded history, such as

division by an earthquake of a large area A into two sub-areas A_1 and A_2 . We might expect taxa in areas A_1 and A_2 to be sister taxa. We might carry out a cladistic analysis of four taxa, one each from areas A_1 and A_2 and two other areas B and C. If we found that taxa in A_1 and B are sister taxa, and A_2 and C are sister taxa, and both pairs together form a monophyletic group, there might be several explanations for this pattern of relationships:

- our cladogram is wrong, perhaps based on characters that are environmentally determined and do not accurately reflect phylogeny; or
- our cladogram is correct, but has nothing to do with recently recorded geological events.

How could we test these two alternatives? The first alternative seems attractive because we might feel intuitively that if an area has been divided, taxa in its subdivisions should be most closely related. If they are not, we might consider reasons for our erroneous cladogram. But, we stated previously one condition under which a cladogram might be doubted: if taxa exhibiting it do not conform to a particular pattern. In this hypothetical example, however, we as yet have no pattern because we have looked at relationships within only one group. Thus, particular characters used in phylogeny reconstruction may be doubted for other reasons, but not because they result in a cladogram that does not correspond with one set of geological events.

To test the second possibility, we may search for some other, older set of geological events that correspond with the cladogram, and claim that these earlier events caused the inferred phylogeny, but we may never find such an alternative geological hypothesis. More important, proposing or not proposing such a hypothesis would not constitute a test of the phylogeny.

We have only one way of evaluating the second alternative: to search for a pattern among members of the biota of areas A_1 , A_2 , B, and C. If we constructed cladograms for five different groups in the biota and they are all the same as for our first group, that is taxa in areas A_1 and B are sister taxa, as are taxa of areas A_2 and C, we would have discovered a general pattern for the biota. What caused this pattern? We may search for an explanation and find one that is suitable, such as, for example, that area A, like North America, should be treated as two (or more) areas of endemism for biogeographic studies. Whatever explanation we choose, we know that our initial prejudice about affect of a known geological event could have led us to believe something that had little support. It is unjustifiable to say that a major prediction of cladistic or vicariance biogeography is that '... concordant cladograms should result from concordant vicariance sequences ...' (Endler 1982, p. 450), because,

histories of areas are complex and involve sequences which we may never recover in any geological study. Furthermore, every vicariant event will not result in a dichotomy in a cladogram. Any biogeographic study that ignores analysis of pattern is faulted because it precludes the search for a general explanation.

3.4.2 Cladograms of areas

What refutes a cladogram of areas? So far, we have considered cladograms of areas that were derived from cladograms of taxa. A cladogram of areas for the hypothetical biota of the preceding section would require that areas A_1 and B be sister areas, and A_2 and C be sister areas. Another way of deriving a hypothesis for history of the areas would be to ask a geologist to construct one. Because configuration of areas (including limits of what we call a continent) changes over time, a geologist may produce several hypotheses, each one for a different period, but none in conflict with the other; that is, no one hypothesis precluding another. We may decide that a geological event separating areas A_1 and A_2 did not produce the general pattern, and that we were perhaps wrong in thinking of area A, which may have been a continent such as North America before the geological event, as one homogeneous area. The geologist may look further into history of these areas and discover that areas B and C are more alike than A_1 or A_2 in a certain set of characteristics, and suggest that because of these similarities, B and C share a history that A_1 and A_2 do not. Consider the possibility that because areas A_1 and A_2 have been joined as a continental land mass, they now have similar geological characteristics. What the geologist discovered that B and C share may be those characteristics that A_1 and A_2 no longer express because the characters have been modified. What B and C share are possibly older geological characters that would not form the data base for construction of a geological cladogram.

Do geologists produce geological cladograms based on derived geological data, or phenograms based on overall similarity of regions? Biologists have little or no expertise by which to judge geological data. Surely sometimes the basis on which two areas are hypothesized to share a close history are derived characters analogous to such characters in biological studies. How significantly changes in the suspected primitive or derived nature of geological data affect current geological hypotheses will only be known in time. Any geological hypothesis is to be approached with the same caution or scepticism one might have for a phylogenetic hypothesis; each should be subjected to rigorous test.

But, can a geological cladogram be tested with a biological cladogram? No, say the majority of vicariance and cladistic biogeographers (e.g. Rosen

1978; Nelson and Platnick 1981; Patterson 1981a). Biological and geological hypotheses have been termed 'reciprocal illuminators' (Rosen 1978); they enhance but do not test one another.

If we consider again the example of taxa in Areas A₁, A₂, B, and C, we understand that a cladogram can only be tested with additional biological data or reanalysis of data used to generate that hypothesis. Similar tests can be made of geological cladograms by reassessing or using new geological data. Failure of a biological cladogram to agree with a geological cladogram for the same areas of endemism should in no way diminish our belief in either, but it should make us scrutinize the two sets of data.

If we believe that the world and its biota evolved together, then we should expect geological data to correspond with biological data at some level. In so far as cladistic analyses of plants and animals have only been applied rigorously to a small (but ever increasing) percentage of groups and to an unknown extent in geology, our expectation may not be realized for generations.

3.5 CONCLUSIONS

In surveying some practical problems one might face in carrying out a cladistic biogeographic analysis, we have touched upon those topics that have traditionally plagued biogeographers (as, for example, estimating age of a group) and presented ways in which a cladistic biogeographer might approach solution of these problems.

Cladistic biogeography centres on historical explanation for distribution patterns. Because no one biogeographic study touches on all problems, we have discussed both real and hypothetical examples. Conclusions from such a variety of examples are diffuse, so we present a summary of the principles of this chapter as a list.

1. Any biogeographic analysis (whether primarily historical or ecological) must consider analysis of pattern.
2. Patterns, congruent cladograms for various unrelated groups, are what need to be explained in biogeographic analysis, not distribution of individual groups.
3. Historical biogeographic analysis constitutes the search for pattern, whereas ecological analysis constitutes the search for individual responses to relatively recent events (namely, nonconformity to a pattern).
4. A vicariance event is anything that disrupts a biota (e.g. divides it into two or more subunits).
5. Vicariance events may be geological (e.g. an uplifted mountain range),

- climatological (e.g. a glacier), or of any other factor that disrupts a biota.
6. Biogeographic analyses must be based on sound phylogenetic studies.
 7. Conformation to pattern is of primary importance in biogeographic analysis. Dispersal capabilities of individual taxa are secondary, and irrelevant if all taxa conform to a particular pattern.
 8. Nonconformity to a pattern may result from random dispersal, ecological variation, or conformity to a different pattern.
 9. As an explanation for a distribution pattern, random dispersal is unique to a taxon, not to a biota.
 10. The present distribution of plants and animals in the world has been caused by a variety of phenomena (including geological history, climate, extinction, dispersals, and introductions).
 11. A biogeographic pattern is a summary of area relationships specified by congruent cladograms of taxa.
 12. All taxa, regardless of their presumed age or inferred dispersal ability, are treated equally in deriving biogeographic patterns.
 13. Amount of congruence among cladograms of taxa is the extent to which they agree, that is, the extent to which they support a particular pattern.
 14. An area initially treated as one in a biogeographic study may be subdivided into two or more areas if relationships within the biota dictate such a division (e.g. if all taxa of a particular group in the initial area do not constitute a monophyletic lineage).
 15. A pattern for a biota conflicts with another pattern for the same biota if one or more area relationships in the first pattern is contradicted in the second.
 16. A fossil representative gives a minimum estimate of the age of a group.
 17. One estimate of the age of a group is the minimum age estimated for the oldest taxon in the general pattern of which it is a part.
 18. A general explanation for a pattern applies equally to all taxa supporting the pattern.
 19. Finding a pattern for some elements of a biota predicts that other taxa in the biota will also conform to the pattern.
 20. Taxonomic level (rank) of a particular group in the biota is irrelevant.
 21. Groups of plants and animals in the same area (a biota) that share a cladistic pattern share a history.
 22. One role of fossils in cladistic biogeographic studies is to help reject geological hypotheses suggesting particular patterns.
 23. Geological hypotheses of area relationships are no more or less reliable than area cladograms derived from biological data.
 24. Geological hypotheses do not test biogeographical patterns.
 25. On some level, histories of areas derived from biological and geo-

logical data should agree; none the less, area relationships based on biological data may be independent of geological relationships of the same areas.

26. A cladogram of taxa can be refuted by other characters, especially if constructed originally on wrong or doubtful characters, but not by geology.

4

A new view of the world

4.1 INTRODUCTION

Integration of cladistics and biogeography developed from the understanding that theories of biogeography, as well as those of systematics, must be testable to be scientific and, therefore, to be incorporated into theories of earth history. But, we gain little from integration of the two fields unless it can tell us something new about the world.

For over a century, naturalists, in particular systematists, have recognized, proposed, and debated numerous theories on the origin of similar biotas of highlands of tropical New Guinea, subtropical New Caledonia, and temperate areas of southern South America, New Zealand, Tasmania, and Australia, sometimes also including the southern tip of Africa (see, for example, Darwin 1859; Hooker 1860 and summarized in Turrill 1953; von Ihering 1900; Eigenmann 1909; Croizat 1952, 1958, 1964; Hubbs 1952; Darlington 1957, 1965; Cracraft 1982; Craw 1982). Along with the Recent and fossil biota of Antarctica (see Grande and Eastman 1986), these areas comprise what biogeographers term the austral zone. Because derivation and distribution of the austral zone biota continue to be the focus of biogeographic studies (e.g. Darlington 1965; Brundin 1966; Keast *et al.* 1972; Good 1974; Cracraft 1982, 1991; Craw 1982, 1985; Diamond 1982; Weston and Crisp 1987; Howes 1990; Carpenter 1993), we have chosen the austral zone, spanning the Pacific, as an example of one large, well known, relatively well-studied region to which methods of cladistic biogeography can be applied.

Examples of groups with austral distributions, in whole or in part, include southern beeches of the genus *Nothofagus* (Humphries 1981; Tanai 1986; Philipson and Philipson 1988; Hill and Read 1991; Hill and Jordan 1993; Linder and Crisp 1996; Veblen *et al.* 1996; Figs 4.1 and 4.2), galaxiid fishes (McDowall 1964; Rosen 1974), mordaciid (biting) lampreys (see map in Berra 1981), southern eel-cods of the family Muraenolepididae (Howes 1990), vespid wasps (Carpenter 1993), pines of the genus *Araucaria* (e.g. monkey puzzle and hoop pine), flowering waratahs of the genus *Telopea* (Weston and Crisp 1987), and many other plant groups as in Du Roi (1940, 1960) and Thorne (1972).

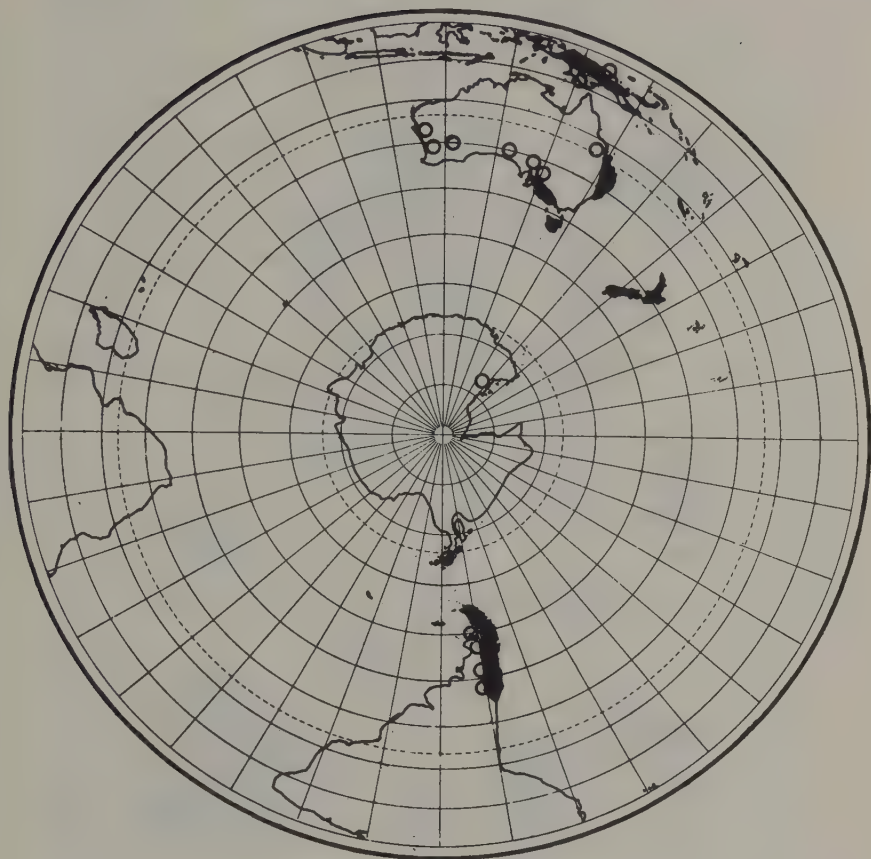


Fig. 4.1 Distributional limits of the southern beech genus *Nothofagus* (after Humphries 1981). Areas inhabited by Recent species are blackened; circles represent fossil localities.

At the same time, biogeographers have debated theories on origins of antitropical distributions; that is, distributions characterized by a close relationship between taxa in the north temperate or boreal zone and taxa in the austral zone (Darlington 1965; Briggs 1987b). Such distributions are often also termed bipolar. In the previous edition and reprinting of *Cladistic Biogeography*, we used the term 'amphitropical' for this distribution, following Darlington (1965) and Rosen (1974). Here, we acknowledge that antitropical is a more appropriate word (see Cox 1990) and use it in this edition.

Examples of groups with antitropical distributions include many remarkable Coleoptera taxa (such as devil's coach horse beetles, gymnosine



Fig. 4.2 *Nothofagus brassii* van Steenis from Papua New Guinea (van Steenis 1953, fig. 5).

staphylinids; Hammond 1975), carabid beetles (e.g. Broscini, Derodontidae, Byrrhinae, Nemonychidae; Crowson 1980), the spiny-finned fish family Percichthyidae *sensu* Berra (1981; Fig. 4.3), crowberries of the genus *Empetrum*, lampreys, midges (Brundin 1966), atherinopsine silverside fishes (White 1985), and the eyebright genus *Euphrasia* among numerous plant taxa (Du Reitz 1940; Thorne 1972).

Dispersalist (McDowall 1964; Darlington 1965), vicariance (Rosen 1974), panbiogeographic (Croizat 1964; Craw 1985; Grehan 1991), and cladistic biogeographic (Humphries 1981; Weston and Crisp 1987; Howes 1990; Linder and Crisp 1996) studies have been carried out, proposing or debating theories to explain distribution of one or more animal or plant group inhabiting austral zone land masses and ocean basins. Whereas these

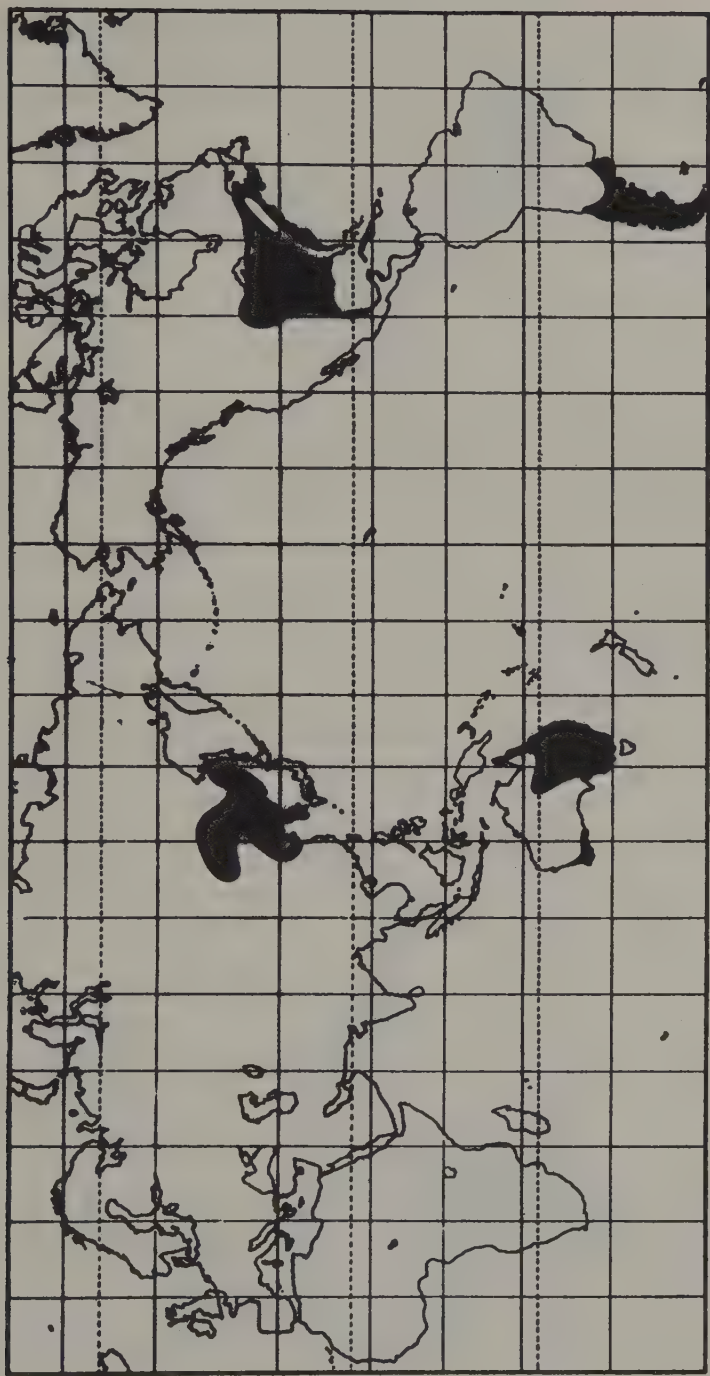


Fig. 4.3 Distributional limits of the percomorph (spiny-finned) fish family Percichthyidae (following Berra 1981).

discussions disagree on methods of analysing austral distributions they have one common element—necessarily limited consideration of how origin of austral zone distribution is related to origin of antitropical distributions, and global patterns as a whole.

Our purpose in this chapter is to integrate these two closely related problems in biogeography into one hypothesis for the origin of global biogeographic patterns, and in doing so exemplify methods of cladistic biogeography.

4.2 TROPICAL VERSUS ANTITROPICAL

An antitropical distribution, by definition, is one in which taxa are present in northern and southern hemispheres, in particular boreal and austral zones, but absent from the tropics (e.g. Hubbs 1952; Darlington 1965). Conversely, pantropical distributions are those with taxa in all tropical regions, but with no representatives in cold-temperate austral and boreal zones.

Pantropical distributions are approximated in numerous groups of animals (e.g. killifishes, cichlids, pomacentrids, some labrids, and nandids among fishes; plethodontid salamanders; and sungrebes) and plants (e.g. nutmegs, Myristicaceae, Indian bean tree family, Bignoniaceae, and ebonies (*Diospyros*)) (see Fig. 4.4). Antitropical disjuncts are also numerous. Of living floras, for example, Thorne (1972) indicates that at least 65 plant genera occur both north and south of the American tropics; amongst these are *Agoseris*, *Amsinckia*, *Bahia*, *Clarkia*, *Gilia*, *Haplopappus*, *Plectritis*, and *Schedonnardus*. Thorne also mentions that a dozen or more plant genera show bipolar disjunctions and amongst these are *Armeria*, *Empetrum*, *Hippuris*, *Koenigia*, *Phippsia*, and *Primula*.

Boundaries between the tropical and boreal zone in the northern hemisphere and between the tropical and austral zone in the southern hemisphere are not precise. Some taxa characterized as tropical, such as *Diospyros* (Fig. 4.4), coexist with typical boreal groups, such as the bog species, *Scheuchzeria palustris* (Thorne 1972), in northeastern North America. Nonetheless, a taxon generally can be classified as a member of a tropical north and south temperate or bipolar group because of its relationship to other taxa and their distribution.

A question biogeographers have asked since the distinction between tropical and north and south temperate groups was noticed is: how did disjunct north and south distributions come about? Answers to this question have involved climatic change (Hubbs 1952; Darlington 1965; Rosen 1974; White 1986), earth history (Nelson 1986), long-distance dispersal from northern North America (Raven and Axelrod 1972; Thorne 1972),

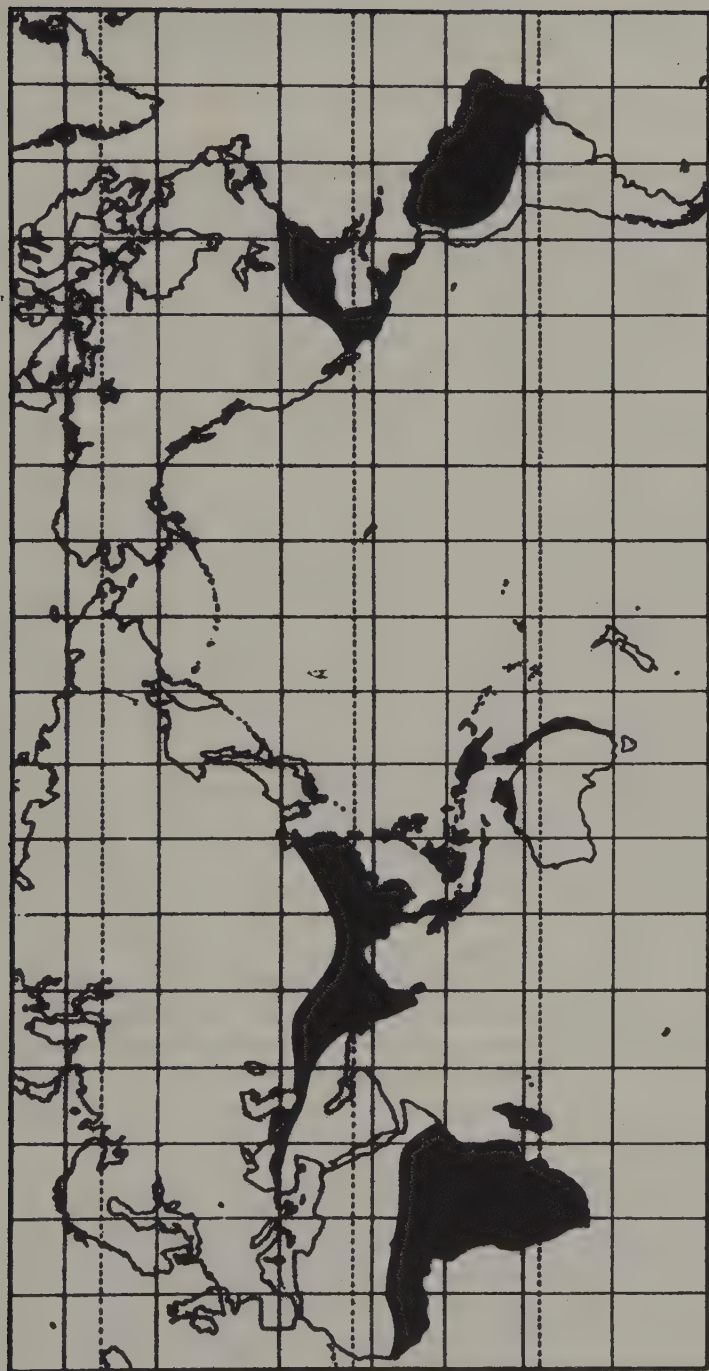


Fig. 4.4 Distributional limits of the pantropical ebonies *Diospyros* (s.l.) (after Thorne 1972).

marine biotic interchange (Lindberg 1991), and bipolar differentiation (Du Reitz 1940.)

Darlington summarized his thinking on origin of disjunct, global distributions as follows:

All together, a large proportion of the plants and animals of the southern cold-temperate (austral) zone are involved in amphitropical distributions at one taxonomic level or another, and they include many of the most characteristic southern groups that are supposed by some persons to have dispersed by means of continental drift or Antarctic land bridges. But the amphitropical pattern cannot be primarily a product of ancient geography. No biogeographers would seriously suggest (or would they?) that existing north and south temperate areas once formed a single land mass entirely separated from existing tropical areas, and that the amphitropical groups of plants and animals are still distributed according to the ancient division of land. Climate apparently must be primarily concerned in formation of the amphitropical pattern.

Darlington 1965, p. 130

The importance of climate in determining where an organism can live today is self-evident; a warm-adapted organism cannot disperse into a cold region and survive. If it does disperse and survive, evolutionary theorists would say it is both warm and cold adapted, and that climate has little to do with formation of zones of distribution on a global scale. Importance of climate in determining how distributions came about is not obvious, especially when relationships of taxa within antitropical groups, and their relationship to tropical groups, are studied.

Bipolar differentiation, that is independent formation of similar groups of taxa at both poles, was postulated initially by numerous biologists in the early nineteenth century (see Du Reitz 1940 for a thorough review). As the theory of evolution became more widely accepted, it was proposed instead that these biotas were in fact closely related. Hence, long distance migration from one pole to the other was suggested and still remains a popular hypothesis to explain antitropical distributions (e.g. Thorne 1972.)

Independent bipolar derivation and migration from one pole to the other by members of each bipolar group were considered highly unlikely, and parts of both theories were combined into one comprehensive theory of cosmopolitanism by Du Reitz (1940). Rather than postulating individual migrations, he stated:

... it seems to be equally possible for a genus or any taxonomic unit to differentiate or 'crystallize' out of its more polymorphic ancestral syngameon simultaneously over a very large area. If such a very polymorphic syngameon was once distributed both in the North and the South as well as over connecting transtropical highland bridges, it would be unnecessary to assume any transtropical migration for bipolar units later differentiated and isolated within this syngameon. And even the very polymorphic syngameon out of which they were differentiated may have flowed as a

broad stream from previous syngameons with a similar distribution, so very old that any speculations as to whether they first came from the North or from the South would be futile.

Du Reitz 1940, pp. 230–1

This concept of ancestral cosmopolitanism and separation from the tropical zone by transtropical highland bridges is similar to Darlington's theory of zonation by climate in that it implies near exclusion of bipolar groups from the tropics. Neither Darlington nor Du Reitz examined relationships of tropical zone taxa to bipolar taxa, therefore they did not question how monophyletic groups of tropical taxa came to be 'wedged in' between sister taxa of the austral and boreal zones.

Cladograms of relationship have not been worked out for many antitropical taxa, and few or no such hypotheses were available to Darlington when he produced his monograph on distributional history of the southern end of the world, or to Du Reitz when he speculated on the origins of bipolar distributions. During the past three decades, cladistic hypotheses have been proposed for several antitropical plant and animal groups. We examine some of these to arrive at an explanation for antitropical distributions.

One group at the forefront of numerous biogeographic studies is the southern beeches, the genus *Nothofagus* (Fig. 4.2) (see Humphries 1981; Linder and Crisp 1996). *Nothofagus* is confined to the southern hemisphere in what we have already referred to as a typical austral distribution (Fig. 4.1). *Nothofagus* is unambiguously represented in the fossil record of Antarctica (Romero 1986; Carlquist 1987; Hill 1987, 1991). At the time of Humphries' (1981) study, *Nothofagus* was considered the sister genus of the north-temperate North American and Eurasian *Fagus*. Nixon (1989) re-evaluated phylogenetic relationships within the larger Fagales, and concluded that *Nothofagus* should be excluded from the family Fagaceae. *Nothofagus* was reclassified in the Nothofagaceae and considered the sister group of northern hemisphere birches, the family Betulaceae, in one phylogenetic hypothesis (Nixon 1989, fig. 3.1). Interestingly, the biogeographic pattern is altered little by the newer phylogenetic hypothesis; *Nothofagus* still has a disjunct, boreal sister taxon, now Betulaceae rather than *Fagus*.

Hill and Jordan (1993) and Linder and Crisp (1996) produced cladograms of the areas inhabited by *Nothofagus* in the austral zone and *Fagus* in the boreal zone; we modify this cladogram to reflect the sister group relationship of *Nothofagus* and Betulaceae (Fig. 4.5). *Nothofagus* species of the Patagonian Andes (South America) are most closely related to a group including representatives in New Zealand, Tasmania, and Australia, which in turn are closely related to a second group of Australian, New Guinean, and New Caledonian taxa.

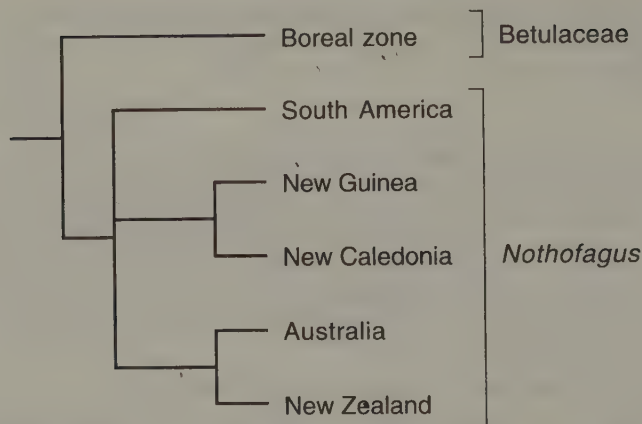


Fig. 4.5 Area cladogram of *Nothofagus* of the austral zone (after Linder and Crisp 1996) and proposed sister taxon, boreal birches, Betulaceae (following Nixon 1989).



Fig. 4.6 Male *Chironomus plumosus* L. (Oliver, in McAlpine *et al.* 1981, p. 423).

The area cladogram for *Nothofagus* and Betulaceae has properties that are found in other groups with antitropical distributions. One is that there is a monophyletic group of austral taxa whose sister group is the monophyletic north-temperate taxon (e.g. Lovis 1989). This is seen again, for example, in the midge family Chironomidae (Fig. 4.6). Brundin (1966), in his monograph on phylogenetic relationships and distribution of certain



Fig. 4.7 Area cladogram of podonomine and diamesine midges (after Brundin 1966).

chironomids, established these midges as a classic example of an anti-tropical group. Chironomids are represented in South America by two sympatric, distantly related subfamilies, Diamesinae and Podonominae. Relationships among areas inhabited by both subfamilies can be summarized in a single cladogram (Fig. 4.7).

Central Andean midges have their closest relatives in the Patagonian Andes. This group in turn forms a trichotomy with midges in Australia and New Zealand. South Africa is the sister area of these three. The austral midge taxa together comprise a monophyletic group. They are the sister group of the monophyletic boreal taxa of Asia, North America, and Europe. Central Andean midges might be considered tropical rather than austral; the Central Andes is considered here along with austral zone distributions because of close relationship between central Andean and Patagonian taxa (see below).

Congruence of north-south relationships and distribution of two groups of midges and the beeches persuade us to explain this distribution pattern. First, we review current theories of earth history to see if past land connections explain the pattern.

4.3 PANGAEA, PACIFICA, OR EXPANDING EARTH?

Existence of an ancient supercontinent Pangaea, comprising all known global land masses that split apart and drifted away from each other to form the current configuration of the continents, is a theory that was proposed formally by German scientist Alfred Wegener (1915, 1929). Sub-division of Pangaea, starting in the Mesozoic and continuing to the present

day, has been the basis of continental drift theory, modified by geologists into a theory of crustal evolution known as plate tectonics. Reluctance among geologists and biologists until recent decades to accept the concept of an unstable crust is now a classic story of resistance to new interpretations of earth history (see Hallam 1973; Nelson 1978). Once sea-floor spreading and plate tectonics, mechanisms for drift, were proposed, acceptance of drift was rapid, and nearly universal among scientists by 1975 (LeGrand 1988). Today, there are few geologists or biogeographers who doubt the reality of plate tectonics, although the field is still alive with debate about sequence and timing of continental separations and collisions (Howell *et al.* 1985).

Darlington (1965) provided a comprehensive, pre-plate tectonics review, but did not accept a former supercontinent, and considered only that South America and Africa were joined at one time in the past, a hypothesis supported by matching between present-day Atlantic margins of the two continents.

There are two more speculative alternatives to Pangaea, itself a model based on the idea that the earth has had constant dimensions. The second theory includes explanations for apparent distributions of continental fragments around the Pacific margin. The third theory argues for an 'expanding' earth to make better fits of continents during the Triassic and Jurassic overcoming the problem that too much of the earth's surface has been swept under continental carpets by subduction than present-day facts allow. In turn, there are at least two versions of the expanding earth theory; fast or rapid expansion and slow expansion.

The second theory (Jones *et al.* 1982; Schermer *et al.* 1984; Howell *et al.* 1985) suggests that major continents do not grow slowly and steadily, gradually accumulating 'rings' of rocks around their margins. Instead, growth of continents is episodic. Jones *et al.* (1982) describe geological and geophysical evidence to suggest that, on the western coast of North America for example, huge prefabricated blocks are grafted piecemeal on to existing continent margins. Almost all of the Pacific coast of North America, from California to Alaska, consists of 20 or more added continental blocks, or terranes, which were carried thousands of kilometres east and north, originating from a remote Pacific basin site. Lengths of these terranes ranged from hundreds to thousands of kilometres.

Jones *et al.* (1982) give no precise clues as to the origin of the terranes but there seem to be two explanations for their present-day existence. Tozer (1982), for example, has a palaeogeographic theory based on distribution of Triassic marine fauna. During the Triassic, the western North America was interpreted as a tectonically quiet coast bordered by an open ocean. Well offshore, a series of volcanic archipelagos shed sediments into adjacent basins. The islands were within 30° latitude of the Triassic equator and

extended offshore for about 5000 kilometres, to the spreading ridge directly ancestral to the East Pacific rise. Geography west of the ridge was considered similar. During the Jurassic, new crust generation at the ridge pushed some islands into the North America plate, some to South America, others westwards to Asia. Tozer suggests also that New Zealand, northern New Guinea, and New Caledonia were at a latitude of 30° north in the Triassic. Terranes of the western cordilleras of North America, he assumed, reached the North American plate before the end of the Jurassic.

This second explanation includes a general theory comprising the former land mass and break-up of a southern supercontinent, Pacifica, now comprising bits of terrane distributed around the Pacific ocean margin. As its name implies, Pacifica was a hypothetical continental mass, the initial rifting of which opened the Pacific ocean. Supporters of this theory propose it in part as an alternative to the Pangaeian model of continental break-up (Nur and Ben Avraham 1981). Thus, under the theory of Pangaeian break-up, the Atlantic was opened by rifting continents; whereas under the theory of Pacifica break-up, the continents were joined in some other fashion, with the Pacific formed by rifting continents.

In the third theory, Carey (1976, 1988), Owen (1976), Shields (1979, 1983, 1991, 1996) and Ellsmore (1991) argue that most Pangaeian reconstructions assume an earth of modern dimensions. For them such reconstructions produce major continental fit anomalies in the Arctic, Caribbean, Mediterranean, and south-east Asia. They suggest that ocean-floor spreading history of these areas and adjacent oceans indicates that they have grown by areal expansion since their initiation. Reconstructions for Cenozoic eras of an earth of constant dimensions assume subduction to account for poor fit of continental margins. There is debate over whether evidence supports much subduction (see Lovis 1989, for example). Owen (1976) shows that an exact fit of various continental fragments together reforms Pangaea, which agrees with geometric and geological matches, and is obtained where the value of the earth's curvature is increased to the point at which the diameter of the earth is 80 per cent of the current mean. This corresponds in time to the late Triassic-early Jurassic and has interesting consequences. Shields (1979, 1983), for example, argues that earth expansion would close the Pacific entirely prior to the Mid-Mesozoic, which means that the Pacific ocean opened as late as Jurassic times.

Each theory competes over arrangement of land masses in a supercontinent and details of timing of rifting. As we wrote (and rewrote) this monograph, a consensus of biologists and geologists favoured the Pangaeian hypothesis, whereas the Pacific islands and Pacifica and the expanding earth hypotheses have been looked upon with scepticism (e.g.

Edmunds 1981; McKenna 1983), in much the same way as many scientists viewed the Pangaeian hypothesis over 30 years ago.

Either supporters of the Pacific islands and Pacifica hypothesis are correct, or supporters of the Pangaea hypothesis are correct, or all are at least partly correct, where problems of timing are overcome by expanding earth models. What can biogeographers do to help resolve the controversy?

Plate tectonics has been viewed as support of vicariance biogeography: if continents have drifted apart then so have plants and animals living on them. A theory of the sequence of splitting of a supercontinental land mass predicts relationships of biotas on land masses. The Pacifica hypothesis predicts close relationship of biotic elements on allochthonous terranes on either side of the Pacific ocean (e.g. parts of western North America and Asia); the Pangaeian hypothesis predicts close relationship of biotas on either side of the Atlantic ocean (e.g. eastern North America and Europe). Vicariance and cladistic biogeographers have tested the Pangaeian hypothesis by comparing their phylogenies to a sequence of the separation of land masses (e.g. Rosen 1974; Humphries 1981; Parenti 1981b; Kluge 1987; Brooks and McLennan 1991; Amorim 1992). Many groups fit the sequence well, at least in part, such as killifishes and cichlids; others, such as midges, do not. In general, pantropical, terrestrial groups fit the sequence of Pangaeian break-up rather well, whereas antitropical and trans-Pacific groups do not.

Numerous examples of trans-Pacific relationships among plants in support of the Pacifica hypothesis were presented by Melville (1981, 1982). These included buttercups in New Zealand and South America, carrots, *Oreomyrrhis*, across the southern Pacific and in the Andes from Colombia to northern Argentina, and shrubby *Coriaria*, *Gunnera*, and the southern speedwells, *Hebe*, in Chile and New Zealand. Seberg (1988, 1991) has documented trans-Pacific distributions, especially in the Cyperaceae. Shields (1983) noted that trans-Pacific links are many and supported a Jurassic split for the Pacific. These include the Microhylinae, a subfamily of small tree frogs, the mole genus *Urotrichus* in Japan and California, and snake subfamilies Xenoderminae and Pareinae (Colubridae) in eastern Asia and tropical America. Crayfish distributions and various south-east Asian groups suggest connections of east Asia with North America and south-east Asia with Australia and Madagascar.

Thus, some biogeographers have claimed that biotic relationships support the Pangaeian hypothesis, whereas we, like Carey (1976, 1988), Melville (1981, 1982), Nur and Ben Avraham (1981), Shields (1983), and Nelson (1986) make alternative claims that relationships represented in other groups support a more recent (Jurassic) Pacific opening as in the Pacifica or expanding earth hypotheses. Because we believe there must be one theory, rather than three or more, to explain worldwide distribution of

biotas, we address the problem of historical biogeography at the southern end of the world to analyse further these three hypotheses.

4.4 HISTORICAL BIOGEOGRAPHY OF THE SOUTHERN END OF THE WORLD

Consistent with foregoing discussions, the Pacifica, expanding earth, and Pangaea hypotheses are probably not competing hypotheses, but all true, at least in part. Differences among these competing theories can be seen from analyses of distribution patterns in southern continents, and their relationship to those of the boreal zone, the problem of antitropical distributions.

4.4.1 Darlington's view (1965)

Despite pleas of Croizat (1952, 1958, 1964), van Steenis (1962), and Craw (1982) that ancient geography demands independent interpretations of present-day distribution patterns, many present-day biogeographers simply accommodate Darwinian dispersal hypotheses on to fashionable geological theories rather than attempt to find general explanations for biological and geological data. Raven and Axelrod (1974, p. 539) went as far to say that:

... plate tectonic theory does not require any modifications of previously established major principles of evolution.

For example, their view of the southern end of the world is simply a modification of Darlington's (1965) view. By this they mean that plants originated in a 'centre of origin' (west Gondwanaland) and then migrated by overland dispersal routes. For them, the austral flora and fauna originated in South America:

Australasia remained open to immigration from South America by island stepping stones for plants and animals of cool temperate requirements into the mid-Tertiary.

Raven and Axelrod 1974, p. 635

In other words, they present no critical appraisal of plate tectonics by biogeographical patterns. To us, Darlington's work best sums up the problems of traditional, dispersalist biogeography. His view of distribution of the biota of the southern end of the world was limited by at least two assumptions:

- (1) a pre-plate tectonic version of geology—that is, since late Cretaceous, southern continents have not been in contact with each other (or connected by land-bridges); and
- (2) a taxonomic group is as old as its earliest fossil representative.

Because many plant and animal groups are not represented by fossils as old as late Cretaceous, Darlington concluded that each group found on southern continents got there by dispersal from its own centre of origin. As distinct from Raven and Axelrod (1974), Darlington admitted that there were conceptual difficulties with postulating dispersal of a variety of organisms across water gaps, but he stated that he was 'forced' (p. 158) to this conclusion by other evidence of age of groups and prior continental contact. He reviewed several possible mechanisms of dispersal, judging some (such as transport on ice floes) to be nearly impossible, and others (such as transport by strong circumpolar winds) to be quite important in creating southern hemisphere distributions.

By keeping to two assumptions of age of groups and lack of relatively recent connection of southern continents, Darlington was forced to conclude that dispersal had been the prime factor in creating distribution of the southern continental biota. His assumptions precluded a precise examination of organism relationships and a search for patterns among relationships. Also, Darlington's method, and that of fitting a phylogeny to a model of Pangaeian break-up, cannot lead to suggestions for reinterpretations of prevailing geological theory because they are wholly dependent upon prevailing theory. We examine this problem further by concentrating on competing biological and geological theories concerning South America.

4.4.2 Two (or more) South Americas

We return to the historical biogeographic study of the southern beech genus *Nothofagus* by Humphries (1981). He presented the area cladogram of Fig. 4.8 as a summary of historical relationships of land masses inhabited by austral and boreal groups, based on cladograms of relationships of many plant and animal taxa, incorporating his data with those compiled by Patterson (1981a). Humphries concluded that eastern North America and Europe are sister areas, and that there is a group of austral areas comprising New Zealand, Tasmania, Australia, New Caledonia, and New Guinea. South American taxa either have close relatives in the northern hemisphere, that is in North America or Europe, or they have relatives in the southern hemisphere, in Australia and associated areas, or relatives in other tropical areas, such as tropical Africa (see also Crisci *et al.* 1991).

The area of South America included in the austral zone is Patagonia, that is, South America south of approximately 30° south latitude. Most lowland tropical South American taxa have affinities with other tropical groups, or with northern hemisphere biotic elements. Craw and Weston (1984) identified several novel geological predictions by Croizat (1958, 1961) that have received independent corroboration from geologists. Perhaps the most outstanding example is of Croizat's plate tectonic model



Fig. 4.8 Area cladogram summarizing data for austral, boreal, and pantropical groups, showing the disjunct relationships of the South American continent (after Humphries 1981).

for the Americas, including a Pacific origin for the western portions of the continents (Croizat 1961). Similarly, Humphries (1981, p. 205) concluded independently that:

The two positions for South America . . . are probably due to the fact that it is a huge composite area and should not be treated as a single area of endemism.

Because South America has affinities with northern hemisphere and southern hemisphere elements, Parenti (1981b) concluded that it should be divided into two regions for biogeographical analysis. These regions were referred to as South America 1 and South America 2 (Fig. 4.9); although precisely where the continent should be divided was not specified. Likewise, Crisci *et al.* (1991) identified southern South America as part of the austral biota distinct from northern South America. The identification of four conflicting hypotheses of relationships of southern South America to other austral land masses led those authors to conclude that southern South America itself may be further divisible into smaller areas of endemism.

Another explanation for different patterns within South America is that taxa more closely related to extracontinental taxa may be relatively older. Older Pacific and Atlantic north-south connections were affected differently by past land connections; the more recent South American groups show relationships to North American, European, and lowland tropical African taxa.



Fig. 4.9 Area cladogram summarizing data of Patterson (1981a) for austral, boreal, and pantropical taxa, showing the disjunct relationship of the South American continent (after Parenti 1981b.)

We examine some evidence in favour of both of these hypotheses, hybrid areas and different ages of biotas, and then review how cladistic biogeography presents information derived from a phylogenetic analysis as hypotheses that corroborate or refute such conclusions.

4.4.2.1 Patterns of taxa

It is clear from relationships of South American taxa to those in the rest of the world that present-day ocean basins, not continents, are meaningful global biogeographic regions or realms (Croizat 1958; Craw and Page 1988; Parenti 1991). Springer (1982) plotted the distributions principally of Pacific basin shorefishes and identified the Pacific plate as an area of endemism. South America is part of three basins: Pacific, Atlantic, and Southern oceans (Fig. 1.14). South American taxa have closest relatives across the Pacific or Caribbean, the southern cold-temperate region (e.g. Australia and other land masses or ocean basins of the austral zone), or the Atlantic, in tropical Africa.

Patterson (1981a) and Humphries (1981) reviewed data on relationships of several widespread groups to search for patterns of distribution of marsupials (Patterson) and southern beeches (Humphries), both represented in South America. Distributional data were presented as area cladograms; that is, cladograms of taxa were redrawn with the name of the area inhabited by a taxon replacing the taxon name (see Chapter 2). The area cladograms repeatedly show South America with at least two associations (Fig. 4.10). South American taxa may have as their closest relative a member of a North American–European or African group, rather than an Australian–New Guinean group (Fig. 4.10a), as in hyliid tree frogs, large

flightless ratite birds and galliform (game) birds, and xylofine flies. Alternatively, South American taxa are more closely related to taxa in Australia and New Guinea than to taxa in North America or Europe (Fig. 4.10b) as in southern beeches, and two subfamilies of chironomid midges. Any cladogram summarizing data given in Fig. 4.10a and b must, like Fig. 4.8, show South America in a hybrid position between the austral region (including Australia and New Guinea) and the boreal region (North America and Europe), or as two separate areas, as in Fig. 4.9.

South American taxa with the pattern of Fig. 4.10a are found typically in tropical lowlands or Andean highlands north of 30° south latitude minus the central Andes. South American taxa with the pattern of Fig. 4.10b are found in South America south of 30° south latitude, in Patagonia. These latter taxa are part of typical austral zone distributions.

That Patagonia contains a biota distinct from that of tropical lowland



Fig. 4.10 (a) Area cladogram of coincident land masses inhabited by hylid frogs, ratite and galliform birds, and xylofine flies (after Patterson 1981a). (b) Area cladogram of coincident land masses inhabited by beeches of the genera *Nothofagus*, and podonomine and diamesine midges (after Patterson 1981a).

South America has been recognized nearly as long as distinctness of the austral zone has been recognized (see von Ihering 1900; Eigenmann 1909). *Euphrasia* occurs in western Patagonia southward from approximately 30° South latitude. It is not a member of the tropical lowland biota and therefore would not be expected to be closely related to North American taxa, given the general pattern of Fig. 4.8.

Many taxa of the central Andean biota have circum-Pacific, extra-continental, affinities (Thorne 1972). Nine taxa of embothriine waratahs, distributed as in Fig. 4.11, are related as in Fig. 4.12 (Weston and Crisp 1987). The central Andean waratahs are in a trichotomy with one group of taxa from New Guinea and Australia and a second group from Australia and Tasmania. The killifish genus *Orestias*, abundant in Lake Titicaca and widely distributed throughout the Altiplano, has been hypothesized to be related most closely to a Eurasian, not South American, killifish genus (Parenti 1981a, 1984); that extracontinental relationship of *Orestias* has been confirmed with phylogenetic systematic analysis of molecular sequence data (Parker and Kornfield 1995). The carabid beetle tribe Cicindini comprises two species, one in Cordoba province, northern Argentina, its sister species near the mouth of the Tigris and Euphrates (Kavanaugh and Erwin 1991). The diatom *Cyclotella andina*, known only from Lake Titicaca on the Peruvian-Bolivian Altiplano, is most closely related to *C. omarensis*, an



Fig. 4.11 Distribution map of embothriine waratahs. Numbers correspond to taxon distribution limits (after Weston and Crisp 1987, Fig. 5).

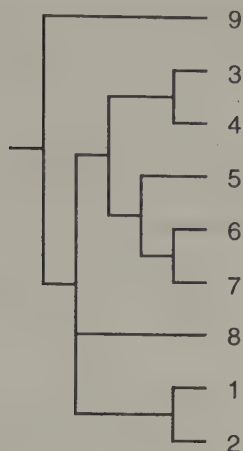


Fig. 4.12 Area cladogram for embothriine waratahs (after Weston and Crisp 1987, Fig. 4). Numbers refer to areas in Fig. 4.11.

Upper Pliocene species from the Kama River basin, a tributary of the Volga River which empties into the Black Sea (Loseva 1981; Theriot *et al.* 1985). Theriot *et al.* (1985, p. 386) concluded:

That a living member of an otherwise extinct group of *Cyclotella* is abundant in the high Andean Lake Titicaca is an indication that there may be much to learn about the South American freshwater diatom flora.

We agree, and add that there is much to learn about its flowering plants, fishes, and carabid beetles as well. Clarification of the relationship of the Andean biota to the rest of the world remains an outstanding problem in biogeography.

4.4.2.2 Patterns of areas

The distinct biological history of Patagonia and possibly also of the central Andes is established. We may consider these areas to comprise the South America of Fig. 4.10b. But what does this biotic distinctness mean for history of the continent?

Area relationships as indicated by taxa in the southern continents and their boreal relatives, and their relationship to taxa in the pantropical zone, may be summarized in general area cladograms (Fig. 4.13a and b, respectively).

Four implications are that:

- (1) taxa in the central Andes are more closely related to Patagonian or extracontinental taxa than to lowland South American taxa;

- (2) central Andean and Patagonian taxa, together, are members of an austral group related to both South Africa and to the Australian region (including New Guinea, New Caledonia, New Zealand, and Tasmania);
- (3) closest relatives of the austral groups are found in the boreal zone. Members of the boreal zone are related in the following pattern: Asia is most closely related to western North America, eastern North America is most closely related to Europe, and these two pairs are in turn sister areas (see also Grande 1994);
- (4) closest relatives of the austral and boreal groups are found in the pantropical region.

This view of the world as presented in one area cladogram (Fig. 4.13b) is derived from relationships among plants and animals. If we believe that the world and its biota evolved together, this summary of area cladograms should be able to tell us something about historical relationships of land

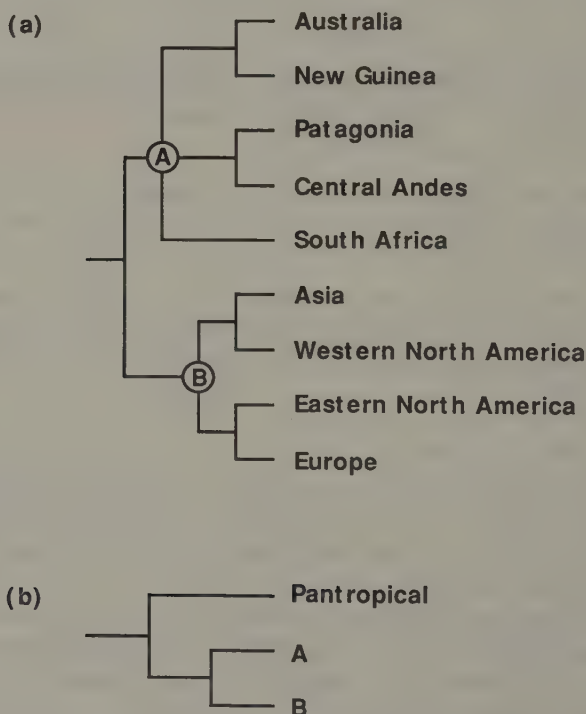


Fig. 4.13 (a) Area cladogram for taxa on the southern continents, or austral zone (A) and their boreal relatives (B). (b) Cladogram summarizing relationships of A and B to taxa in the pantropical zone.

masses. The relationship of austral and boreal groups to pantropical groups has implications for the type of model of earth history one believes is supported by such patterns of biotic relationships. For example, even though phylogenetic relationships of the spiny-finned percichthyid fishes (*sensu* Berra 1981), an antitropical group, are still under debate (see, for example, J. S. Nelson 1994), one prediction of the general pattern is that, if the Percichthyidae is monophyletic, northern hemisphere taxa form a monophyletic group that is the sister group of a monophyletic southern hemisphere taxon. This would require trans-Pacific relationships in both the northern and southern hemispheres. It would also require trans-Atlantic relationships in both hemispheres, and agree with the former existence of an Atlantic continent. No single theory of continental splitting, Pacifica, expanding earth, or Pangaea, agrees in total with what relationships of taxa suggest to us about past land connections. We could derive an independent theory of land mass relationships from geological data. On some level, we expect area cladograms derived by systematists to be congruent with relationships of land masses derived by geologists.

Can geological information be used separately to derive a theory of relationships of southern hemisphere land masses? We continue to look at one continent, South America, in detail.

The central and southern Andes are characterized by rock (estimated to be as old as the Jurassic) lying on top of continental South America. These regions were termed 'Peruvian Pacifica' and 'Magellanian Pacifica' by the botanist Melville (1981) (Fig. 4.14). The same areas are approximated by the South American waratahs (Fig. 4.11; areas 8 and 9). But why 'Pacifica'?

In a review of geologic history of the Andes, geologist Werner Zeil (1979) stated that the Andes of Colombia, Ecuador, and Venezuela fit the plate tectonic model for the history of South America, and correlate with classical hypotheses of Andean mountain building by subduction of a Pacific plate. The Andes of Peru, Bolivia, Chile, and Argentina, Zeil argued, do not correspond to the plate tectonic model. To quote Zeil (1979 p. 193):

The wealth of morphological features is a reflection of the geologically different elements which make of [sic] the coastal range of the Andes.

He characterized the Andes in Colombia and Ecuador as remnants of a late Mesozoic island arc or oceanic crust welded to the central and eastern Cordilleras of the continental Andes. The central and southern parts of the range (Peru, Chile) are continental crust without typical oceanic material but probably consist of a large number of different tectonic segments.

Other geologists have opposed or debated this explanation. We emphasize that geologists disagree on particular facts relating to an area's history in the same way as systematists disagree on relationships among taxa. Important questions, such as whether or not South America fits the plate tectonic



Fig. 4.14 Map showing two regions of South America, Peruvian and Magellanian Pacifica, postulated by Melville (1981) to be derived from an ancient Pacific continent.

model, are still unanswered. For example, James (1973), in his hypothesis for evolution of the central Andes, comments on this Jurassic Peruvian rock, stating that:

... the rocks could be part of a Paleozoic microcontinent or peninsula that lay to the west of the South American coastline; or they could be sialic flotsam swept into and plastered to the edge of South America, buoyant debris scraped from the top of the oceanic plate as it dived down at the trench.

James 1973, p. 65

Nur and Ben Avraham (1981) had little doubt that exotic terranes found around the Pacific margin, including at least part of the central and southern Andes, are of an ancient Pacific continent they termed Pacifica. Alternatively, other geologists (Batten and Schweickert 1981) and palaeontologists (Tedford 1981; Tozer 1982) had little doubt that these terranes had nothing to do with an ancient Pacific continent. Jones *et al.* (1982) reviewed history of trans-Pacific land masses, especially those of North America and Asia, and concluded that western North America has grown by collisions with small land masses, some of which originated far west of the present continent.

As biologists, we are unable to evaluate different theories proposed by geologists for history of these land masses. To derive a cladogram from

geological data including the central and southern Andes, certain questions must be answered: are rocks of the Peruvian and Magellanian Pacifica of the same origin? That is, are their similarities derived similarities that would indicate shared geological history? If so, to what land mass are they next most closely related; that is, what land mass shares unique properties with the Peruvian and Magellanian Pacific? And, is the land mass continental or extracontinental? Without answers to these questions biologists can only suggest that their cladograms of taxa accurately reflect earth history. Biological evidence indicated continental drift well in advance of its eventual acceptance (see also Croizat 1961; Grehan 1991). Geologists, as well as biologists, should re-examine their theories to see if their hypotheses really are good fits to geological facts.

4.4.2.3 Geology or age?

Separate biotic associations of tropical and temperate southern South America suggest at least two conclusions: South America is a continent of hybrid origin; or there is an older and younger component to these patterns, that is, the association of part of South America with the austral zone represents a distribution pattern of older groups which has since been overlain by younger groups that have affinities with other tropical representatives.

Biological data represented by area cladograms (Figs 4.5–4.9, 4.10, 4.12) present a considerable challenge to geologists to address problems that prevent full understanding of the geological history of South America, as we have discussed above (see also Craw 1989a; Grehan 1991).

Can relative ages of groups aid our understanding of origin of South American relationships? It is true that many pantropical groups fit a model for the break-up of Pangaea rather well. These groups also tend to be relatively young. For example, killifishes, which fit the Pangaeian model to a great extent, are represented by fossils as old as the Oligocene (Parenti 1981a). Antitropical groups tend to be relatively old; beeches (Humphries 1981), beetles (Crowson 1980), and midges (Brundin 1966) are at least as old as the Jurassic. That these groups are at least as old as the Jurassic suggests that the pattern of Fig. 4.13b may be this age. This follows from the idea that if we recognize a pattern, all taxa sharing the pattern came to occupy the same areas at the same time in response to the same geological events. If this is not true, then any other taxon sharing the pattern and represented by younger fossils would have to have formed the same distribution pattern at a later date. Parsimony precludes this conclusion. That is the nature of a pattern in cladistic biogeography.

Now, with estimates of ages of taxa, and hence of patterns, we conclude that antitropical distributions of beetles, midges, beeches, *Euphrasia*,

lampreys, and percichthyids, among other taxa, are older than pantropical distributions (shared by cichlids, killifishes, pomacentrids, and ebonies, among others). That antitropical distributions are older will remain our conclusion until an even older fossil is found in the pantropical zone which is a member of a group conforming to a Pangaeian break-up pattern. Briggs (1987b) also concludes that antitropical taxa are relatively old relicts.

Geologists could aid us by suggesting relative ages of continental separation or movement of exotic terranes. Considerable effort has been put into understanding the ages of terranes in the Pacific (see Chamberlain and Lambert 1985). Ages of the Pangaea model in its many formulations was reviewed by Humphries (1981). The supercontinent is estimated to have started breaking up in the Jurassic or even the Triassic. In the fast-expanding earth model, Shields (1979, 1983) estimates initial opening of the Pacific in an expanding earth model as Jurassic. Thus, geological estimates really do not help much in deciding which pattern of break-up occurred first, or if they were concurrent.

4.4.3 A composite New Zealand

Cladistic biogeography is not concerned solely with sequences of fragmenting biotas as determined by plate tectonics; it is concerned ultimately with an explanation for composite areas (Platnick and Nelson 1984). As demonstrated by Croizat (1952, 1958) and elaborated by Craw (1979, 1982, 1989a,b) and others, 'track' as well as cladistic analyses show that in addition to North and South America, areas such as New Zealand have complex biogeographic patterns, exhibiting a variety of overlapping relationships with neighbouring or with distant areas (see Schuh and Stonedahl 1986; van Welzen 1989 for the Indo-Australian archipelago). The studies of Craw (1989a-c), Dugdale (1989), Heads (1989), Southey (1989), Tangney (1989), and Grehan (1990, 1991) suggest that New Zealand taxa are part of at least 15 generalized tracks which traverse the Indian, Pacific, and Southern oceans.

To explain the geology, Howell (1980) proposed that New Zealand is composed of four exotic terranes—microplate accretions along the Gondwanian margin—two related to Australia and Pacifica and two of uncertain origin. Later, Cooper (1989) hypothesized that New Zealand is composed of 13 separate coalesced terranes which belong to six major groups (Figs 4.15, 4.16). The oldest, the Tuhua terrane, dates from the Devonian, 350–400 million years ago. Of particular interest to biogeographers, the Torlesse terrane (Fig. 4.16) is of exotic origin, possibly from the Marie Byrd Land Jones mountains of west Antarctica, and the others have accreted gradually through time. To explain biogeography and geology together, Craw (1989a) proposed a parallel arcs model for the

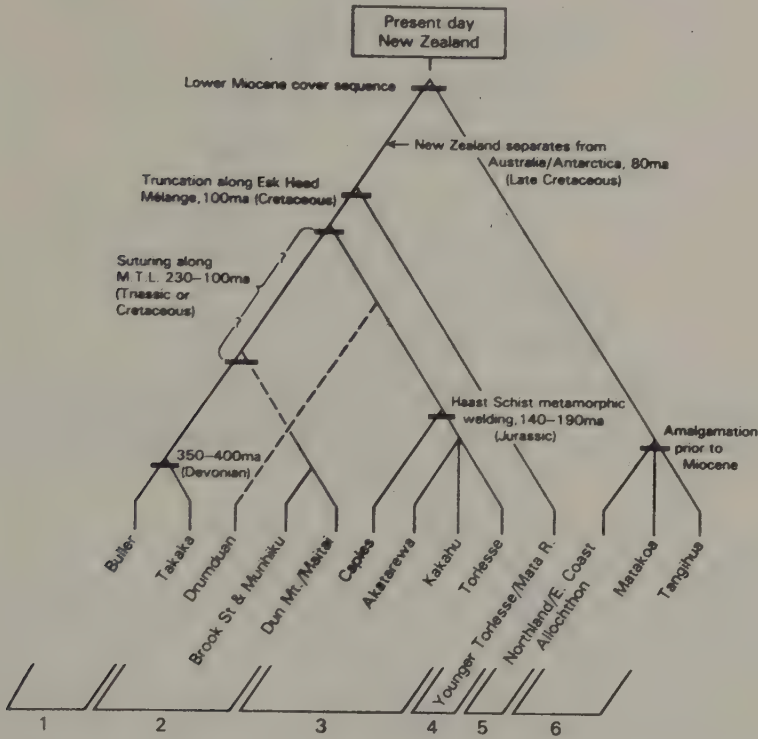


Fig. 4.15 Branching diagram of New Zealand terranes based on an interpretation of geological history. Terranes are coalescing, rather than diverging, over time. Nodes represent suturing events, with the oldest events at the bottom, youngest events at the top (from Cooper 1989, Fig. 3). See Fig. 4.16 for further identification of the terranes.

evolution of New Zealand: initial geographic separation of two adjacent biotas and associated features, tectonic bending and fragmentation, and finally the distinction between the western and eastern arcs on the North, South, and Chatham islands. Grehan (1991) has elaborated on the panbiogeographic analyses of New Zealand to show that the geological complexity of the arcs and biogeographic tracks are nested. Further, phylogenetic relationships of New Zealand taxa across the Pacific, Indian, and Southern oceans are expected, given New Zealand's physical relationship to all three oceans (Craw 1989a, fig. 19) (Fig. 1.14).

How do cladograms based on geological data compare with cladograms of taxa? Figure 4.17a and b give two simplified patterns for three areas for five widely different groups. The first pattern is formed on the basis of two plant groups: *Nothofagus* (Humphries 1981) and a combined cladogram for

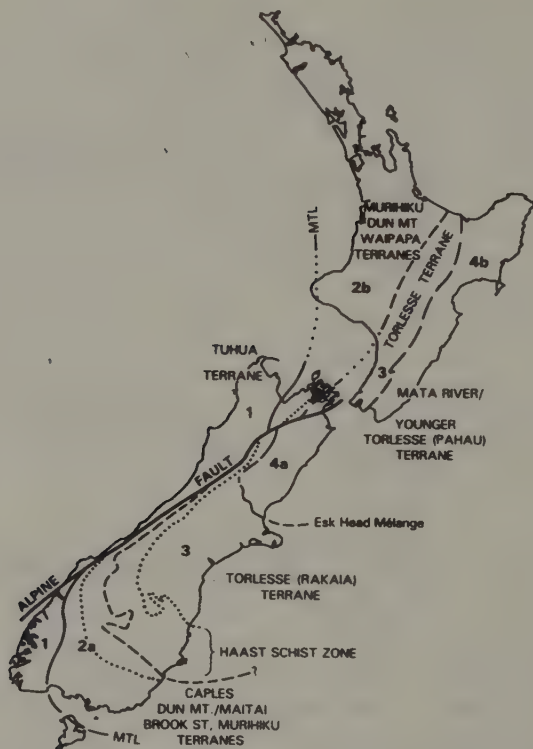


Fig. 4.16 New Zealand terranes (from Cooper 1989, Fig. 1). (1) The late Paleozoic Tuhua terrane; (2) the five late Paleozoic–early Mesozoic volcanogenic terranes, Caples, Dun Mountain–Matai, Brook Street, Murihiku, and Drumduan, are grouped (2a) and shown in the the same zone as the Murihiku, Dun Mountain, and Waipapa terranes of the North Island (2b); The position of the 2a/3 boundary is approximate, being obscured by the later Haast Schist zone (Haast Schist and Aspiring terranes); (4) Younger Torlesse terrane (4a) is regarded as equivalent to Mata River terrane (4b).

three genera of Persooninae (Weston, in Craw 1982). The second pattern is more common, as shown by a combined cladogram of four genera of Gesneriaceae (African violets; Humphries 1981), a genus of caddis-flies (*Hydrobiosella*; Ross 1950), and a group of platycercine parrots (Craw 1982). The two patterns, if viewed superficially, are incongruent. What does this mean biogeographically? If continental fragmentation is considered, treating New Zealand as a single area would suggest that *Nothofagus* and Persooniinae are uninformative. That is, the cladograms for three groups, *Hydrobiosella*, Gesneriaceae, and parrots agree with a continental break-up pattern, but, the cladograms for *Nothofagus* and Persooniinae are incongruent with such a



Fig. 4.17 Reduced area cladograms. (a) *Nothofagus*; Persooniinae (*Persoonia*, Australia; *Toronia*, New Zealand; *Garnieria*, New Caledonia). (b) *Hydrobiostella*; Gesneriaceae (*Fieldia*, Australia; *Coranthera*, *Depanthus*, New Caledonia; *Rhabdothamus*, New Zealand); and platycerine parrots.

pattern. This view is geologically naïve, however. If New Caledonia consists of a minimum of two continental fragments, one of which separated from Australia during the Jurassic, and the other of which separated as a result of opening of the Tasman Sea during the Upper Cretaceous–Palaeocene, then groups associated with older and younger sequences would naturally be incongruent (Craw 1982). As Craw noted, the *Nothofagus*/Persooniinae pattern (Fig. 4.17a) would be associated with the Jurassic fragment, whereas the second pattern (Fig. 4.17b) is due to rafting of a biota in the north-east Australia–New Caledonia/New Zealand track.

4.5 A NEW VIEW OF THE WORLD

Darlington (1965) was ‘forced’ to conclude that climate and dispersal were primary factors in establishing both antitropical patterns and similarity of biotas on southern continents because he made two assumptions, given above and restated here:

- southern continents were relatively stable during the period of evolution of taxa on the land masses, precluding the existence of a former large supercontinent in the southern hemisphere; and
- taxa occupying these land masses are too young to have been affected by any postulated land movement.

We have discarded these assumptions and seen that an alternative view of the world is possible. Our view suggests a return, in part, to the ideas

of Humboldt and Hooker, as well as Murray (1873), on the importance of former southern hemisphere land connections.

4.5.1 Pacifica and antitropical distributions

So far, we conclude that:

- (1) an explanation of distribution of taxa on southern continents is related to antitropical distributions;
- (2) close relationship of austral groups to boreal groups, rather than to pantropical groups, suggests a former connection between austral and boreal zones; and
- (3) certain aspects of both the expanding earth and Pacifica hypotheses coincide with relationships among antitropical groups.

Biogeographers are still left with an intriguing problem: how does one explain antitropical distributions? If one believes that phylogenetic relationships of taxa can tell us something about the form of past land connections, then the following model is a plausible explanation for antitropical distributions (Fig. 4.18): austral and boreal groups were at one time adjacent, and they in turn were adjacent to a tropical zone. Movement of the austral zone to the opposite side of the tropical zone would present a world called Pangaea, ready to break up at the end of the Triassic to form patterns of relationship of land and taxa consistent with our present hypotheses concerning relationships. Trans-Pacific and trans-Atlantic

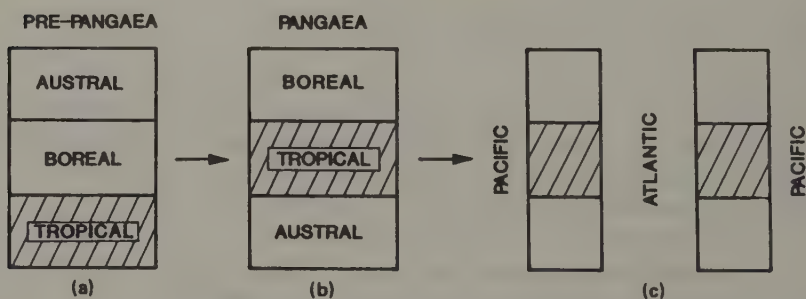


Fig. 4.18 Schematic diagram of hypothetical relationships of austral, boreal, and pantropical zones. (a) 'Pacifica' or pre-Pangean configuration with austral and boreal zones adjacent. (b) Pangean configuration with austral zone having moved to opposite side of tropical zone. (c) Rifting to form Atlantic ocean (earlier division of Pangean continent into Laurasia and Gondwanaland not shown). Earth expansion is one possible mechanism for rifting of Pacifica.

patterns would accompany opening of the Pacific and Atlantic oceans; and these would be austral and boreal.

We term the hypothetical continent in which austral and boreal zones are adjacent 'pre-Pangaea'. We could just as well have called it *Pacifica*, because like all continental masses proposed under that name, it explicitly requires juxtaposition of current trans-Pacific and antitropical areas.

4.5.2 *Pacifica* versus Pangaea: geology or age?

The schematic diagram of Fig. 4.18 is one of many that could be constructed to describe a pre-Pangaean configuration of land masses on a globe. Others have been proposed earlier, primarily by geologists (see, for example, Bambach *et al.* 1980). Although we cannot give a geological mechanism, this model does have an important relative correlation with age. Many antitropical distributions are older than pantropical distributions. We hesitate to give an absolute estimate of timing of events in this model, primarily because both geologists and biologists have presented break-up of a Pacific continent in contrast to break-up of Pangaea, rather than considering that if some sort of *Pacifica* existed, it existed much earlier than Pangaea and, therefore, would be of an older geological period.

4.6 CONCLUSIONS

In this chapter, we have attempted to provide one hypothesis for both antitropical and austral distributions, coordinate problems that have captured the interest of biogeographers for over a century. This investigation has, by necessity, expanded to one in which we examined explanations proposed for the related problem of disjunct distributions of South American and New Zealand taxa.

As cladistic biogeographers, our primary concern is finding a historical explanation for a global distribution. We look first for patterns of relationships among austral and antitropical groups for which reliable cladograms of relationships had been proposed. Our task is made easier by finding a single explanation for cladograms of two subfamilies of midges and beeches of the genus *Nothofagus* and the family Betulaceae, because midges (Brundin 1966) and beeches (Humphries 1981; Nixon 1989) have figured prominently in many studies of austral and antitropical biogeography.

Finding a pattern (Fig. 4.13a,b) corroborated in whole or in part by numerous other groups of plants and animals requires a general explanation for distribution of austral zone and antitropical distributions and for the complex compositions of South America and of New Zealand. In

search of an explanation, we abandon restrictions or assumptions placed on many previous biogeographic studies. These restrictions are:

- (1) that prevailing geological theory (here former existence and break-up of the supercontinent Pangaea) should be the only framework within which our pattern is interpreted; and
- (2) that a group is estimated to be only as old as its oldest fossil representative.

Our pattern for disjunct biotic associations within South America, which includes the hypothesis of close relationship of the central Andes to Patagonia, and hence inclusion of the central Andes in the problem of defining austral and antitropical distribution patterns, correlates in a striking way with hypotheses of some geologists (Carey 1976, 1988; Shields 1979, 1983; Nur and Ben Avraham 1981) and biologists (Croizat 1964; Melville 1981; Nelson and Platnick 1981) for an extracontinental origin of these areas of South America.

Incorporation of a pattern of area relationships of the austral and boreal zones (including an implied relationship of pantropical taxa) with the Pacifica, expanding earth, and Pangaeian hypotheses, poses these separate theories of taxa and area relationship not as independent theories but as part of an integrated whole. It is not the final answer. To some it will not even be a plausible answer, for as Darlington said:

No biogeographer would seriously suggest . . . that existing north and south temperate areas once formed a single land mass . . .

Were it the final answer, biogeography would be over, for we would have explained the world, and we have not done that.

We view the hypothesis of Fig. 4.13b as just one of many that could today be proposed as an explanation of antitropical patterns. The significance of cladistic biogeography in establishing this pattern is that it is not based on one group of organisms, but on a series of distantly related taxa.

We believe that there is just one underlying theory of geological evolution that when proposed will explain most large-scale distribution patterns. That theory will be based on an exhaustive set of both biological and geological cladograms. When cladograms of relationship of all taxa, worldwide, are known, the pattern we have presented in Fig. 4.13b could be the most unusual among all groups of taxa and explicable only by dispersal of individual taxa. But, for now, it is our only hypothesis of antitropical distributions and relationships, incorporating the pioneering cladistic data presented for midges and beeches. As such it remains to be corroborated or refuted by cladistic analyses of additional antitropical groups.

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Glossary

analogue, analogy (cf. *homologue*) similar characters or character states that have different but parallel modifications from other conditions, e.g. wings of birds and bats.

antitropical (bipolar) a distribution characterized by taxa present in the northern and southern hemispheres, in particular the boreal and austral zones, but absent from the tropics (= *amphitropical* of Humphries and Parenti 1986).

apomorphy derived from (and different from) a generalized condition; used of characters, e.g. apomorphic characters.

area a biogeographic region occupied by a monophyletic group of organisms or a species.

area of endemism an area recognized by concordant distributions of two or more organisms.

austral zone temperate regions of the southern hemisphere.

biogeography the study of what organisms live where on earth and why.

biota all the plants, fungi, animals, microorganisms, etc. occupying a given location.

bipolar see *antitropical*.

boreal zone temperate regions of the northern hemisphere.

centre of origin in dispersal biogeography, the area in which a taxon is supposed to have evolved, hence, from which it has dispersed.

cladistic biogeography the combination of cladistics (phylogenetic systematics) with vicariance biogeography. A method that searches for patterns of relationship among areas of endemism.

cladistics (phylogenetic systematics) a method of phylogeny reconstruction concerned with branching patterns. Sister group relationships are hypothesized on the basis of shared derived, or synapomorphic, characters.

cladogram a branching diagram specifying the hierarchical relationships among taxa; the terminal nodes (or taxa) and the internal nodes are defined by apomorphic (derived) characters.

components elements of a group of areas, or group of taxa, as determined by the branching pattern of a cladogram, e.g. in a group comprising three taxa A, B, and C, when B is more closely related to C, there are two components, an ABC component and a BC component.

concordance the degree of agreement between patterns.

congruence agreement in the systematic distribution of characters or topology of cladograms.

consensus tree a branching diagram that conveys the general agreement among components of two or more cladograms for the same taxa or areas (see *strict consensus tree*, *Nelson consensus tree*).

- consistency index (CI)* a measure of fit of characters on a cladogram which is the ratio of minimum possible number of character state changes to the actual number of changes.
- continental drift* see *plate tectonics*.
- cosmopolitanism* former widespread ancestral distribution of a group of organisms prior to vicariance and regional specialization.
- disjunct* distribution characterized by spatial gaps between related taxa.
- dispersal* the movement of an organism from one area to another independent of other organisms and of earth history, which changes the natural distribution of the organism.
- dispersion* the movement of organisms and their offspring within their natural range.
- ecological biogeography* spatial patterns of organisms considered in terms of their interactions with other organisms and the environment.
- endemic* a taxon which is restricted to a given area and found nowhere else in the world.
- expanding earth* the theory that the earth's dimensions have increased through geological history.
- fit* the degree to which the individual components of two cladograms agree, recorded as *items of error* (q.v.).
- Gondwanaland* one of two supercontinents formed by the break-up of the ancient supercontinent Pangaea; comprising the Indian subcontinent, Africa, Antarctica, Australia, New Zealand and South America.
- generalized track* two or more tracks connecting two or more areas of endemism (see also *track*).
- historical biogeography* the study of the history of the distribution of life on earth.
- homologue, homology* (cf. *analogue*) similar characters or character states that share modifications from another condition, e.g. wings of birds in relation to forelimbs of other tetrapods. In cladistic biogeography, areas that share a history are homologous.
- items of error* as a measure of fit, the number of additional nodes and terminal taxa that must be added to one cladogram to make it identical to a second.
- Jurassic* the period of earth history that began approximately 206 million years ago and lasted approximately 65 million years.
- Laurasia* one of two supercontinents formed by the break-up of the ancient supercontinent Pangaea; comprising North America, Greenland, Asia, and Europe (but not including the Indian subcontinent).
- monophyly (monophyletic group)* used of a group which includes all the taxa, and only the taxa, descended from a common ancestor; groups are diagnosed as monophyletic by the presence of synapomorphies.
- Nelson consensus tree* a cladogram that summarizes both the shared and the unique components that do not conflict with or contradict the shared components of two or more cladograms.
- node* terminal and internal branch point on a cladogram.
- Pacifica* an ancient supercontinental land mass composed of bits of exotic terrane now distributed around the Pacific margin. The theory is not accepted broadly by geologists and biologists.
- panbiogeography* the examination of distributions and relationships on a worldwide scale.

- Pangaea* an ancient supercontinent comprising all known continental land masses.
- pantropical* groups of organisms distributed throughout the tropical zone and absent from the austral and boreal zones.
- paralogy* duplication or redundancy in geographic distribution of taxa related by a particular node of a cladogram.
- paraphyly* (*paraphyletic group*) a category or false group based on the common possession of plesiomorphic characters (*symplesiomorphy*); a group which does not contain all of the descendants of a common ancestor.
- parsimony* the logical criterion for obtaining the best supported (i.e. best-fitting) cladogram(s) for a given set of characters.
- pattern* a set of relationships among taxa or areas as specified by two or more cladograms.
- phenetics* a method of systematics that groups taxa on the basis of overall similarity.
- phylogeny* genealogical relationships among all organisms.
- plate tectonics* (including *continental drift*) concept of earth history that the earth's crust is composed of plates that move relative to each other through sea-floor spreading and subduction. As continents are found on plates, continental drift is one result of this movement.
- plesiomorphy* a generalized character or condition shared by all members of a group.
- polyphyly* (*polyphyletic group*) a category or false group based on the common possession of independently derived, but superficially similar, convergent characters (*homoplasy*); a group which contains taxa of different ancestors.
- progression rule* the concept which predicts that the most plesiomorphic members of a taxon occupy the taxon's centre of origin, whereas the more apomorphic members have dispersed away from the centre, such that the more apomorphic a taxon, the farther from the centre it will occur.
- realm* (*region*) an area of the globe occupied by similar plants and animals.
- reconciliation* a method for making one cladogram agree with another by adding or subtracting branches or duplicating internal nodes.
- redundancy* duplication in geographic distribution of taxa on adjacent nodes of a cladogram.
- retention index (RI)* a measure of grouping potential with characters on a cladogram as a ratio of the maximum possible number of changes minus the number of observed changes to the number of maximum possible number of changes minus the number of minimum changes.
- sister taxa* (*areas*) two taxa (*areas*) that are more closely related to each other than either is to a third taxon (*area*).
- strict consensus tree* a cladogram that summarizes the shared components of two or more cladograms.
- sympatry* (*sympatric*) two, or more, taxa occupying the same or overlapping ranges.
- symplesiomorphy* see *paraphyly*.
- synapomorphy* a derived character, or character state, shared by and defining a group of organisms within the context of a large group.
- track* a graph or line which connects two or more areas of endemism on a map.
- transformation series* a series of (three or more) increasingly apomorphic characters or character states.
- Triassic* the period of earth history that began approximately 248 million years ago and lasted approximately 43 million years.

vicariance the existence of closely related taxa or biota in disjunct areas, which have been separated by the formation of a natural barrier (vicariance event).

vicariance biogeography the study of repeated patterns of distribution within many members of a biota that may be explained by vicariance (or splitting) events.

vicariance event the splitting of a taxon or biota into two or more geographical subdivisions by the formation of natural barriers such as mountain building, glaciation, stream capture.

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The distribution and classification of life on earth has long been of interest to biological theorists, as well as to travellers and explorers. Cladistic biogeography is the study of the historical and evolutionary relationships between taxa, based on their particular distribution patterns across the earth. Analysis of the distribution patterns of the taxa in different areas of the world can tell us how the areas are related, what regions or larger groups of areas exist, and what their shared history might be.

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